Competition between plantation *Eucalyptus nitens* (Deane and Maiden) Maiden and naturally regenerating *Acacia dealbata* Link.

(Andrew)

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Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

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(30th November, 1998)

Declarations

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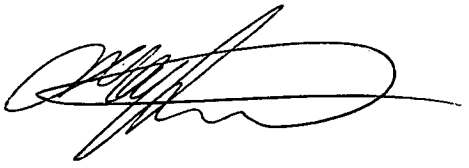

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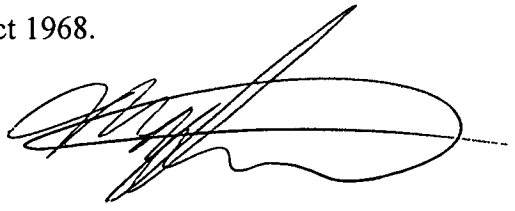

Mark A. Hunt

Abstract

Competition between planted *Eucalyptus nitens* and naturally regenerated *Acacia dealbata* weeds was investigated in an industrial plantation in north-east Tasmania. The effects of this competition on stand growth, canopy architecture, tree water use and leaf gas exchange were considered in 1988- and 1992-planted stands during the period 1994-1997.

Under favourable moisture conditions, *A. dealbata* grew at a rate close to (and sometimes exceeding) that of *E. nitens*. Competition peaked at age 2-6 years before declining as the *A. dealbata* canopy was suppressed, in part by intraspecific *Acacia* competition and consequent self-thinning. At ages 2-4 years, *E. nitens* basal area was highly correlated inversely with both *A. dealbata* stem frequency and basal area. However, by age 6 years, *E. nitens* basal area was not a significant correlate of *A. dealbata* basal area.

The effects of competition on the productivity of *E. nitens* were substantial, reducing standing volume compared to *Acacia*-free plots by almost 25% by age 8 years. Soil nitrogen status was positively correlated with *A. dealbata* presence and negatively correlated with *E. nitens* basal area. *A. dealbata* was therefore considered to be a net contributor of nitrogen but competition for other resources negated any positive effects of this contribution. Silviculture during site preparation and establishment was identified as an important contributor to the distribution and abundance of *A. dealbata* throughout the plantation.

Highly significant regression relationships were developed among leaf area and a number of stem variables for *A. dealbata* and *E. nitens*. Whilst basal area was found to be a suitable predictor of leaf area for both species, the closest relationships were developed between leaf area and sapwood area or cross-sectional area at the crown base. The relationships between basal area and leaf area were used to scale basal area measurements to stand leaf

area index which was partitioned between the two species. In 1995, for nine 7-year-old plots with *Acacia* competition, *E. nitens* had an average stand LAI of 2.6 compared to an average LAI of 4.3 for five plots of the same age without competition. In 1996, for six 8-year-old plots with *Acacia* competition, *A. dealbata* contributed an average 20% of a stand LAI of 3.4. In a single 4-year-old plot, *A. dealbata* contributed 50% of a total LAI of 2.9. In an adjacent *Acacia*-free plot, the LAI of *E. nitens* was 2.5, 86% of canopy LAI in the *Acacia* infested plot (above) but nearly twice that of the eucalypt component of that plot. Estimates of vertical leaf area distribution within an 8-year-old *Acacia*-infested plot indicated that leaf area of *E. nitens* was concentrated between 13 m and 22 m above the ground, whereas leaf area of *A. dealbata* was concentrated between 8 m and 16 m above the ground. Data from transects of vertical irradiance indicated that transmittance was reduced most markedly between 14 m and 20 m above ground.

Computer image analysis was used to investigate the accuracy of measurement of area of the pinnate leaf of *A. dealbata*. Standard planimetry techniques were found to have inadequate resolution for this application. Furthermore, the habit of *Acacia* pinnae closing about the rachis precluded accurate area measurement of the intact leaf. Consequently, reduction of leaves to component primary pinnae was found to be necessary for accurate area determination. The results suggested that, due to these combined errors, stand leaf area of *A. dealbata* may have been underestimated by as much as a factor of 2 in this study. Whilst the magnitude of the underestimation was marked, the direction and consequences of the relationships derived in this study were not affected by application of a correction factor. Hence leaf area data were analysed as measured in the first instance but an alternative measurement protocol recommended for future experiments.

Whole tree water use was estimated using the heat pulse velocity technique during a six week summer period. 4-year-old and 8-year-old trees were considered in *Acacia*-infested

and *Acacia*-free stands as well as stands cleared of *Acacia* competition. Maximum sap velocities were recorded between 5 mm and 15 mm under the cambium for all trees and marked radial and axial variations in sap velocity were observed. The latter source of variation was most pronounced in mixed stands where crowns were asymmetrical. Mean daily sapflux ranged from 1.4 - 103.6 l day^{-1} for eucalypts and from <0.1 - 8.4 l day^{-1} for acacias. Stem diameter explained 98% of the variability in sapwood area for *E. nitens* and 89% for *A. dealbata* and was determined to be a suitable variable for scaling water use from tree to stand level. Transpiration varied from 1.4 - 2.8 mm day^{-1} in *Acacia*-infested 8-year-old plots and was 0.85 mm day^{-1} in an *Acacia*-infested 4-year-old plot. Values of 1.7 and 1.8 mm day^{-1} were returned for two 8-year-old plots recently cleared of *Acacia* competition. The level of *A. dealbata* infestation was associated with absolute plot water use and regression models predicted that in the absence of *Acacia* competition plot water use for the 8-year-old stand would approach 5-6 mm day^{-1} during the growing season.

The maximum photosynthetic rate (A_{max}) for both species was approximately 25 μmol CO_2 m^{-2} s^{-1} and photosynthetic light response curves were similar between species. A_{max} was rarely observed for *A. dealbata*, primarily because of stomatal closure in response to declining leaf water status. The two species responded similarly to soil and atmospheric demand as measured by diurnal variation in stomatal conductance and leaf water potential. However, for *A. dealbata*, reduction of both variables occurred in response to conditions of lower demand than for *E. nitens*.

A. dealbata was concluded to be an important competitor in the system studied, with the potential to markedly reduce the productivity of *E. nitens* over the course of a pulpwood rotation. A number of management prescriptions was proposed that may alleviate competition to the benefit of stand productivity. *A. dealbata* was also found to possess an

unusual life history, occupying a brief temporal niche in disturbance-prone communities where it can persist in the long term as propagules in the soil between disturbance cycles.

Acknowledgments

The research described in this thesis was conducted in a commercial eucalypt plantation owned by Boral Timber Tasmania (BTT). Scaffolding for access to the canopy and technical assistance in the field were supplied by the company when required. Mr Rob McCleland (of Woodstock Forest Services) provided tree-felling expertise for the destructive sampling exercises. Additionally, Mr. Peter Naughton (BTT) provided much background material on site preparation and plantation establishment as well as a useful operational perspective on the research. Messrs. Joe and Shirley Jensen, residents adjacent to the plantation and former owners of the land, also provided very useful historical information about the site.

The research was supported financially, including a Ph.D. scholarship, by the Cooperative Research Centre (CRC) for Temperate Hardwood Forestry (now CRC for Sustainable Production Forestry) from January 1994 until June 1997.

My supervisors, Dr Chris Beadle, Dr Neil Davidson and Mr Greg Unwin, collectively prodded, cajoled and at times dragged me to the project's conclusion. Chris ensured that I always had the necessary resources, instilled an essential practicality into my research and provided great depth of knowledge and sharp critical evaluation. Neil forced me to ask sensible ecological questions and kept me from making the project too applied for the degree. Greg shared my pre-dawn expeditions to the canopy, was a sounding board for my many hypotheses and suffered the brunt of daily triumphs and frustrations of the research. I extend my deepest thanks to all three for their various contributions as well as their friendship.

Mr Dale Worledge initially made everything work, from weather stations to computer software. He leaves me with the knowledge that research scientists provide no more useful function than to amuse technicians with their ineptitude. Mr Jamie Cooper made a similarly important technical contribution to the project, particularly in the canopy where few others were prepared to work with me. Mr John Honeysett assisted with the soil moisture instrumentation and calibration. A number of others provided technical help during the project and of these I would like to thank particularly Ms Maria Cherry, Mr Martin Tyson and Ms Linda Ballard.

I am indebted to Dr Libby Pinkard and Dr Mike Battaglia for providing encouragement, professional criticism and friendship throughout the project.

Dr Don White and Dr Stephen Hodson suffered sharing offices with me. Don's interest in tapirs saved my sanity. Steve is probably the only marine biologist to have worked in a canopy tower. They both have my professional and personal respect as well as my gratitude.

I would like to thank my parents, Irene and David Hunt, for their unwavering support of me in this venture, as has been the case with everything else I have done. My father, particularly, spent countless hours with me in the field, erecting scaffolding, digging holes, recording data and becoming technically proficient with a range of instruments.

Finally, the most important contribution to this work has been the support of my wife Kim and my children, Caitlin and Joseph. Kim supported me unreservedly throughout my undergraduate training as well as my Ph.D. This thesis is dedicated to her.

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Chapter 1. Introduction

This thesis reports and discusses the results of research carried out in the field over three years. The objectives of the research program were twofold. Firstly, a plantation production problem had been identified by a commercial forestry company and required investigation. Financial assistance for the research was provided in terms of the provision of equipment and labour as well as a stipend. The approach required to address the company's concerns was necessarily both applied and empirical. Secondly, and of greater relevance to the requirements of the degree for which this thesis is submitted, were more fundamental questions about the nature of competition in what was essentially a two species system. The primary aim in this instance was for research to be of a basic and mechanistic nature.

Necessarily, these two aspects of the program were inextricably mingled and mutually reliant as will be clear in the following experimental chapters. However, it is useful, both in this introduction and in the concluding chapter of the thesis, to consider them separately.

1.1 The commercial problem - Acacias as weeds.

The genus *Acacia* occupies an equivocal position in production forestry and land management (eg for sand dune stabilisation; Roux and Middlemiss 1963) where commercial and other benefits may be offset by the widespread establishment of many species as weeds. For example, the closely related Australian species, *Acacia dealbata* Link. and *Acacia mearnsii* De Wild. have been grown commercially in South Africa (eg Sherry 1971) and in Asia (eg Fujimori and Yamomoto 1967) as well as in Australasia (eg Frederick et al. 1985) but problems are recognised in their ability to displace native vegetation in exotic environments (Henderson 1989).

Acacia species also compete heavily with desired hardwood species in the secondary succession of cleared native forests. Such competition from *Acacia* in native forests has been considered by a number of authors in Australia where, following severe fires or regeneration burns, some *Acacia* species may germinate prolifically. This is particularly the case in wet forests such as those dominated by *Eucalyptus regnans* F. Muell. (Adams and Attiwill 1984) and *Eucalyptus delegatensis* R.T. Baker (Keenan and Candy 1983).

A. dealbata is considered an 'r' strategist *sensu* Macarthur and Wilson 1967 (New 1984), maturing early and at four to five years of age setting hard seed which may remain in the soil for at least 200 years (Gilbert 1959). The duration and intensity of fire events determine subsequent abundance of *Acacia* seedlings *in situ* (Floyd 1966) though mechanical scarification has been demonstrated by several authors as important for commercial germination of a number of *Acacia* species (eg Aveyard 1968; Clemens et al. 1977). Several studies have considered the effects of fire on soil temperature and consequent *Acacia* germination (Beadle 1946; Floyd 1966). *A. dealbata* may show increased stocking density after hot slow fires in eucalypt forests (Cunningham and Cremer 1965). Following germination, more rapid early growth of *A. dealbata* than that of the more commercially valuable *E. regnans* has also been observed (Ashton 1975). Whilst the presence of *A. dealbata* is a good indicator of site quality (Keenan and Candy 1983), early competition (Cunningham and Cremer 1965) and the ability of the species to persist in the understorey (Adams and Attiwill 1984) may have significant consequences for forest production in the short term.

The potential for *Acacia* species to benefit the nutritional status of the soil has received limited study. Bernhard-Reversat (1988) reported higher mineralisation rates of nitrogen in an *Acacia seyal* Del. stand than under *Eucalyptus camaldulensis* Dehnh. Studies of pure stands of *A. mearnsii* (Venkataramanan et al. 1983) and *A. dealbata* (Frederick et al. 1985)

have demonstrated that litterfall contained 50% and 100% more nitrogen respectively than the eucalypt species with which they were compared. The large amounts of nitrogen and other nutrients immobilised in *Acacia* biomass in native forest suggest that they may represent an important resource when returned to the soil following eucalypt canopy closure (Adams and Attiwill 1984). In long-rotation production forests this is particularly important within the context of their potential value in conserving nutrients and replacing nitrogen lost at the time of harvest.

Short-rotation *Eucalyptus nitens* (Dean and Maiden) Maiden plantations are being established at a rate of 4000-5000 ha a^{-1} in Tasmania (Australian Bureau of Agricultural and Resource Economics, 1994). Establishment is predominantly in areas receiving over 1000 mm annual rainfall and commercial growers have reported significant *A. dealbata* infestation at the more fertile, high quality sites (P. Naughton Boral Timber Tasmania, pers. comm.). Due to the longevity of *Acacia* seed in the soil, both ex-native forest and ex-agricultural sites are susceptible. Whilst *A. dealbata* is a suitable pulpwood species (and may constitute up to 15% of yield for pulping purposes), early competition with the primary plantation species has the potential to reduce yield over the course of a 15 - 20 year rotation. Competitive interactions among plantation *E. nitens* and *A. dealbata* weeds have not previously been investigated. Therefore, quantification of the extent and mechanisms of competition is important for future silvicultural management.

1.2 Fundamental issues of competition

Competition among plants has been defined in numerous ways, two of the most useful being by Clements, "When the immediate supply of a single factor necessary (for growth) falls below the combined demands of the individual plants competition begins" and Bazzaz (1990), "Competition can be viewed as that subset of plant interference interactions that is

mediated through the use of shared resources." Furthermore, Goldberg (1990) (cited in Bengtsson et al. 1994) states that both the effect and response components of competition must be significant and of the proper direction for that competition to be important (see also Grace and Tilman 1990). Thus, where a shared resource is limited, not only is the effect of neighbour plants on resource availability important, but equally so the ability of a target plant to morphologically or physiologically respond to a change in resource availability.

If one accepts the above definitions, it becomes apparent that competition must be for either one or more of light, water, nutrients or carbon dioxide and that the closer any two plants are in their response to these environmental variables, the more intense competition will be between them (Bazzaz 1987; 1990). Consequently, interspecific competition is likely to be less intense than intraspecific competition, and in the latter case most intense for a species with little morphological or physiological plasticity.

Because competition is the result of differential resource acquisition and a plant's capacity to secure resources depends on morphology and physiology, Tremmel and Bazzaz (1993) have defined five mechanisms of competition that can be condensed below as - the manner in which resources are obtained; the way these resources are used to gather more resources; the effect on resource availability to potential competitors; and the plant response to resource preemption. These mechanisms of competition among plants are poorly understood.

Consideration of competition has been restricted traditionally to monocultures, due both to the applicability to issues of thinning and spacing in crop systems and due to the increased complexity at all levels of scale that is inherent in multispecies systems. In such work on monocultures, emphasis has been on communities where competition is assumed to be occurring and changes in individual plant characteristics or in population structure have

been the foci. It is therefore the results of inferred competition that are studied rather than competition *per se* (Ford 1975). Typical of such an approach are experiments that consider presence or variation in frequency distribution of a plant biometric variable, mortality and morphological adjustment of plants growing at different densities (the concept of density dependent stress, see Harper 1967).

The life histories of study plants are also important to the explanation of differences in measured performance (Roberts and Gilliam 1995). Plant communities are dynamic and temporal development is as important as static measurement of density in terms of influence on competition (Ford and Diggle 1981). Initial canopy position, potential benefits of morphological or physiological plasticity or even germination triggers may strongly influence subsequent competitive outcomes (McMinn 1992; Tremmel and Bazzaz 1993).

Hence, qualitative correlation studies are essential to the development of understanding a potentially competitive system and are required for the formulation of sensible hypotheses prior to rigorous experimentation and manipulation (Bell et al. 1991). The importance of initial qualitative studies is made more apparent by recognition of site heterogeneity (and consequent restriction on the number of populations that may be sampled) as an inherent obstacle to the establishment of statistically valid experiments (Ford 1975).

Reliance on statistical rather than qualitative analysis of competition experiments is further hampered by violation of the assumption of statistical independence by individual plants in a population (Ford and Diggle 1981). If one assumes that competition only occurs when interaction among plants is taking place, then independence of samples is a *prima facie* impossibility. Many classical statistical procedures are thus invalidated. Furthermore, there are no strict statistical tests for population features such as bimodality (Rabinowitz 1979),

an important indicator of competition within a population. Interpretation of data is by necessity, therefore, often visual, inferential or by logical argument.

Deficiencies in mechanistic understanding and restrictions in statistical analysis have not precluded the formulation of models to predict yield losses in competitive systems (eg Doyle 1991). However, most models are static and deterministic and consider neither below-ground resources nor self thinning (Benjamin and Aikman 1995). Descriptions of below-ground structure and associated competition are rare, primarily due to the attendant research being notoriously difficult (Bell et al. 1991). However, there is a significant body of literature on self thinning including a number of modelling approaches (see Westoby 1984). Nevertheless the predictive capacity of these deterministic models has been good. This may be attributed in part to the greater importance of above-ground competition identified in many systems (eg Donald 1958; Loomis 1967; 71). Additionally, it is dominant individuals in the weed population that will actively compete with the crop species, and as a within-species hierarchy of competition develops and self thinning occurs, the loss of small individuals from the weed population is unlikely to influence the crop.

Against this background, the following research program was designed to investigate competition between an *E. nitens* plantation crop and naturally regenerating *A. dealbata* weeds.

1.3 Objectives and hypothesis

Undesirable plant species (weeds) in plantation monoculture may reduce productivity of the crop species through competition for one or more of three resources: light, water and soil nutrients. Fast growing eucalypt species under short rotations (<20 years) for pulpwood are particularly susceptible as losses in productivity early in the rotation may not

be recouped by the time of anticipated harvest. Competition is likely to be greatest when the weed species fills an ecological niche close to that of the crop species and patterns of resource use are similar (see above). Accordingly, this thesis addresses four questions related to potential competition between *E. nitens* and *A. dealbata*:

1. Does *A. dealbata* reduce the productivity of the *E. nitens* crop?

2. If so, for what resources do the two species compete?

3. How does the competitive process change over time and if so is there a critical period in the process?

4. What morphological or physiological differences advantage one species over the other?

Therefore, the null hypothesis that this thesis addresses is that the physiological and morphological capacity for *A. dealbata* to actively compete with *E. nitens* is insufficient to bring about significant reductions in eucalypt productivity.

The implications of the results for the management of plantation sites that are prone to competition from *A. dealbata* are also discussed.

1.4 Summary

The thesis is divided into eight chapters, including this general introduction. The contents of the remaining chapters are summarised below:

Chapter 2. Patterns of competition at the stand level

Distribution of *A. dealbata* within the plantation, associated biometric and population characteristics, and effects on *E. nitens* productivity were investigated, particularly in relation to soil nutrition, site preparation, plantation establishment and silvicultural management.

This chapter has been published (in a slightly different form) in Forest Ecology and Management (117:75-85).

Chapter 3. Canopy structure and architecture 1: Specific leaf area and the relationship between stem variables and leaf area.

Differences in leaf morphology (particularly specific leaf area) between the species, in stands of two ages, were studied in consecutive years. Stem variables, including basal area and basal sapwood area, were related to tree leaf area using linear regression. An appropriate scaling variable was identified for consideration of leaf area distribution in the mixed species canopies.

This chapter has bee accepted for publication in New Zealand Journal of Forestry Science (1999, in press).

Chapter 4. Canopy structure and architecture 2: Crown form, leaf area index and the vertical distribution of leaf area.

Leaf area index was calculated from the relationships described in Chapter 3 and apportioned between species. Leaf distribution and crown morphology were related to radiation environment and changes in species dominance during early plantation growth.

Chapter 5. Canopy structure and architecture 3: Accurate area determination of complex leaves using digital image analysis

Sources of error in the determination of individual leaf area were examined and a method developed for overcoming these errors in complex leaves. Leaf area data from the previous chapter were reconsidered.

A slightly different form of this chapter has been accepted for publication in the Australian Journal of Plant Physiology (1999, in press).

Chapter 6. Whole tree transpiration and stand water use partitioning

A combination of recently developed approaches to scaling point measurements of sapflow to stand level was used to investigate the relative contributions of *A. dealbata* and *E. nitens* to total stand water use.

This chapter has been published (in a slightly different form) in Tree Physiology (18:557-563).

Chapter 7. Foliar gas exchange and plant water status

Leaf level ecophysiology was investigated for both species. Diurnal patterns of water use and photosynthesis were related to soil and atmospheric moisture status. Patterns of variation in gas exchange characteristics between species, within crowns and among canopy positions were identified.

Chapter 8. A review of competitive interactions between *E. nitens* and *A. dealbata* and their management and ecological implications

The results of the preceding chapters were discussed within the framework of the hypotheses stated in Chapter 1. Prescriptions for management were developed.

Chapter 2. Patterns of competition at the stand level

2.1 Introduction

Weed competition in plantations is a well recognised and much studied source of reduction in primary crop productivity (Cole and Newton 1986). However, in most systems, competition is from understorey species, particularly grasses or bracken, which fulfil entirely different ecological niches to the plantation tree species. Competition is generally most vigorous during the early establishment phase of the plantation, when fast growing herbaceous species may not only compete for limited nutritional and water resources but also shade young tree seedlings. In close-spaced plantation systems, competition is generally reduced markedly at canopy closure, when understorey competitors are starved of light and consequently are not able to effectively compete with the trees for water and nutrients (Shainsky and Radosevich 1986). In more open canopies, as are typical of plantations grown for wood products, rather than fibre, the understorey may persist indefinitely and provide an ongoing source of competition.

Previous studies of competition have focused primarily on coniferous plantation forests where herbaceous (e.g. Berbigier et al. 1991), woody (eg Spittlehouse and Black 1982) and pteridophyte (e.g. Roberts et al. 1984) understoreys have all received attention. Studies of eucalypt plantations are poorly represented in the literature pertaining to understorey competition, the most comprehensive experiments being conducted in the *Eucalyptus marginata* forests of south-western Australia (e.g. Greenwood et al. 1985; Crombie et al. 1989; Crombie 1992). Furthermore, rarely in plantations is the primary competing weed a woody species similar to the crop species.

A. dealbata is a pioneer species that is well adapted to colonisation of sites prepared for plantation establishment. This species is widely distributed across moist sites throughout Tasmania where it forms a dominant component of frequently burned sites but is restricted primarily to drainage lines and sheltered slopes in more developed communities. Seeds are produced prolifically, generally once every two years, and remain viable in the soil for up to 200 years. Hence, even after extensive forest modification or short-term alternative land-use (eg agriculture), an abundant seed bed may remain in areas with few extant mature trees.

Acacia seeds germinate during site preparation and are at an initial disadvantage to the crop species in terms of root and shoot biomass and height. However, the crop species is generally planted at a wide spacing ($\leq$ 1000 stems ha^{-1}) and canopy closure is not expected until about age 3 years. The initial density of *A. dealbata* weeds will influence the extent to which intraspecific competition and consequent self-thinning will occur but more importantly, the likelihood of early canopy closure (Benjamin and Aikman 1995). As competition occurs between individuals rather than populations (Ross 1981), heavy intraspecific competition among *A. dealbata* stems may reduce the number of individuals of sufficient size to provide effective interspecific competition with the eucalypts.

An increase in height:diameter ratio occurs with a decreasing light environment (Wang et al. 1994; Chen 1997). Should this be identified in stands with high *A. dealbata* density, where *E. nitens* crowns are not contiguous, competition for light will be indicated. Furthermore, changes in the proportion of *E. nitens* stem variables over time will indicate any changes in the magnitude of such competition.

In Section 1.2, emphasis was placed on the importance of qualitative and life history studies for initial assessment of the presence or absence of competition and as a tool in the

design of an experimental program. Hence, in this study, sites were identified across the plantation that exhibited a range of levels of *Acacia* presence, that considered both the earliest and most recent eucalypt plantings and, within the constraints of site heterogeneity, exhibited the least physical variation between treatments. The objectives were to identify:

- the presence or absence of competition between *E. nitens* and *A. dealbata*

- spatial and temporal variation in competitive intensity

- resources for which competition was occurring

and thereby test the null hypotheses that *A. dealbata* does not compete for resources with *E. nitens* and that *A. dealbata* presence does not improve the nitrogen status of the soil.

Whilst the measurement program was intended to extend for the life of the project, initial results were required to design the experimental program reported in subsequent chapters.

2.2 Materials and Methods

2.2.1 Site description

The study was conducted in a commercial eucalypt plantation at Wyena, in north-east Tasmania, approximately 35 km east of Launceston (UGR 55GEQ222374) (figure 2.1). The plantation occupies the head of a small north-facing valley and comprises approximately 38 ha of *Eucalyptus globulus* Labill. and 560 ha of *E. nitens.* All experimental work was conducted in the *E. nitens* coupes. The site has moderate rainfall (*ca* 1000 mm an^{-1}) with generally good but variable drainage due to the presence of Mathinna Shale as the parent rock. Soil depth varies markedly over the site from greater

than 2.5 m in colluvial deposits at low elevations (130 m amsl) to less than 0.5 m at a variety of locations including eroded upper slopes (400 m amsl). The original vegetation comprised wet eucalypt forest dominated by *E. regnans* in gullies and near the valley floor and *E. delegatensis* on the upper slopes with a mixed rainforest understorey. Between 1958 and 1986, 300 ha of the site was used for agriculture, both grazing and cropping systems being employed. The site was converted to plantation forest in the period 1988-1992.

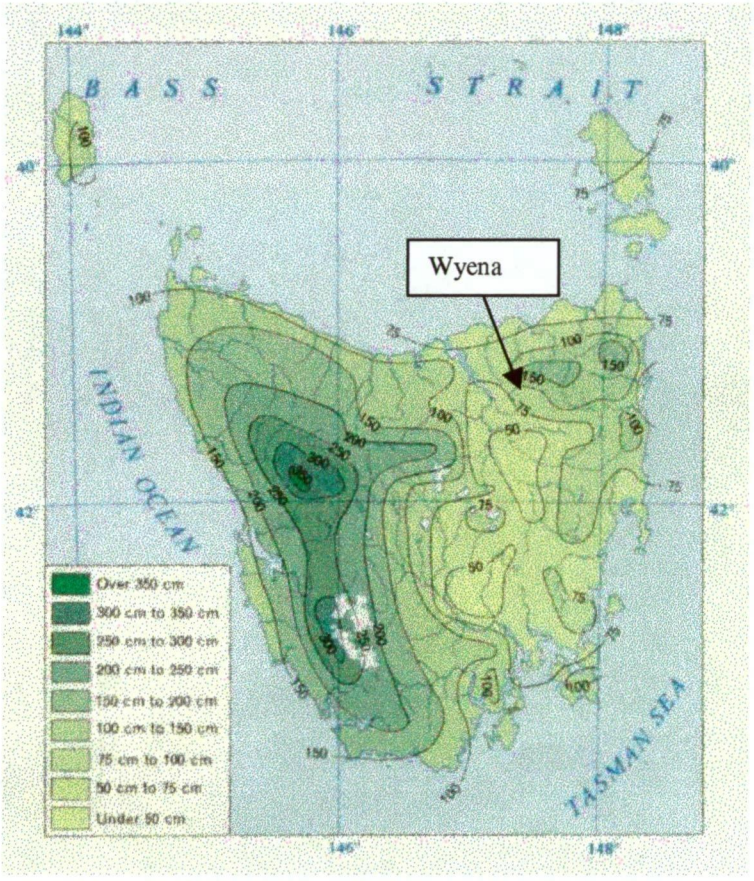


Figure 2.1 Location of the study site in north-east Tasmania close to the 1000 mm rainfall isohyet. (Reproduced from Condon, E.A. 1974. A student's Atlas of Tasmania).

2.2.2 Plantation Establishment

The initial plantings of *E. nitens* in 1988 and 1989 were on ex-pasture sites. A broadcast application of 1.5 kg ha^{-1} of glyphosate (as 'Roundup') was followed by ripping and mounding up and down slopes. A residual herbicide ('Atrazine') was applied at a rate of 3 kg ha^{-1} along the mounds at the first opportunity at a time preceded by 10 mm of rain within the previous week. Planting occurred in September and was followed by application of 200 g fertiliser (4:7:0 - N:P:K) per tree in December. A secondary application of the same fertiliser occurred at the mound bases twelve months later at a rate of 400 g $tree^{-1}$. After 1989, coupes were ripped and mounded along contours.

Plantings after 1989 were on logged sites. These were broadcast burnt after removal of merchantable timber. Ridges and forest edges were burnt initially prior to ignition of the greater proportion of the coupe. This resulted in higher intensity fires towards the centre of coupes and in drainage lines, and lower intensity fires on ridges and edges. Spot planting using motorised augers (as opposed to mounding) was employed on difficult sites (in terms of topography and related management) in the 1992 plantings and accounted for 162 of 270 ha planted that year. Methods of weed control and fertilisation did not vary from those used on ex-pasture sites. The planting stock of *E. nitens* was initially raised from seed of the Upper Toorongo and Rubicon provenances. This seed was collected from native forest. After 1989, seed was derived from a seed orchard at Winkleigh in northern Tasmania. The trees in the orchard were open pollinated and consisted of individuals from the Upper Toorongo, Rubicon and Macalister provenances. The orchard had been established by Forest Resources (now Boral Timber Tasmania Pty Ltd). *E. globulus* was also derived from seed orchards in northern Tasmania (Birallee improved seed).

Hardened seedlings were planted out at a height of 15 – 20 cm at approximately nine months of age. Stocking density at establishment varied from 816 to 1000 stems per hectare. Spacing was nominally 3.5 m x 3.5 m or 4 m x 2.5 m between and within rows respectively.

Vertebrate browsing was controlled by application of 1080 poison. This was undertaken twice yearly during each of the five years in which coupes were planted. A substantial free feeding program preceded poisoning in each instance.

2.2.3 Measurement program

Four experimental sites were established in coupes of *E. nitens* between January 1994 and August 1995 (Figure 2.2). Site 1 was located on an ex-pasture site in a 1988 planting at the base of the valley in deep colluvial soil. An area of 0.28 ha was subdivided into plots for population and growth experiments. *A. dealbata* was present in high density throughout Site 1. *Rubus fructicosa* L. (blackberry) and *Pteridium esculentum* (Forst. f.) Cockayne (bracken) occurred sporadically.

Site 2 was located in the same coupe as Site 1, but at its topographically highest point where soils were shallower. This 0.12 ha site was subdivided into five measurement plots. Only a single tree of *A. dealbata* grew within the site and otherwise no understorey was present. Differing from normal procedure, application of herbicide at this site occurred some months after ground preparation. Aspect and slope were identical to those at Site 1 but Site 2 was generally more exposed.

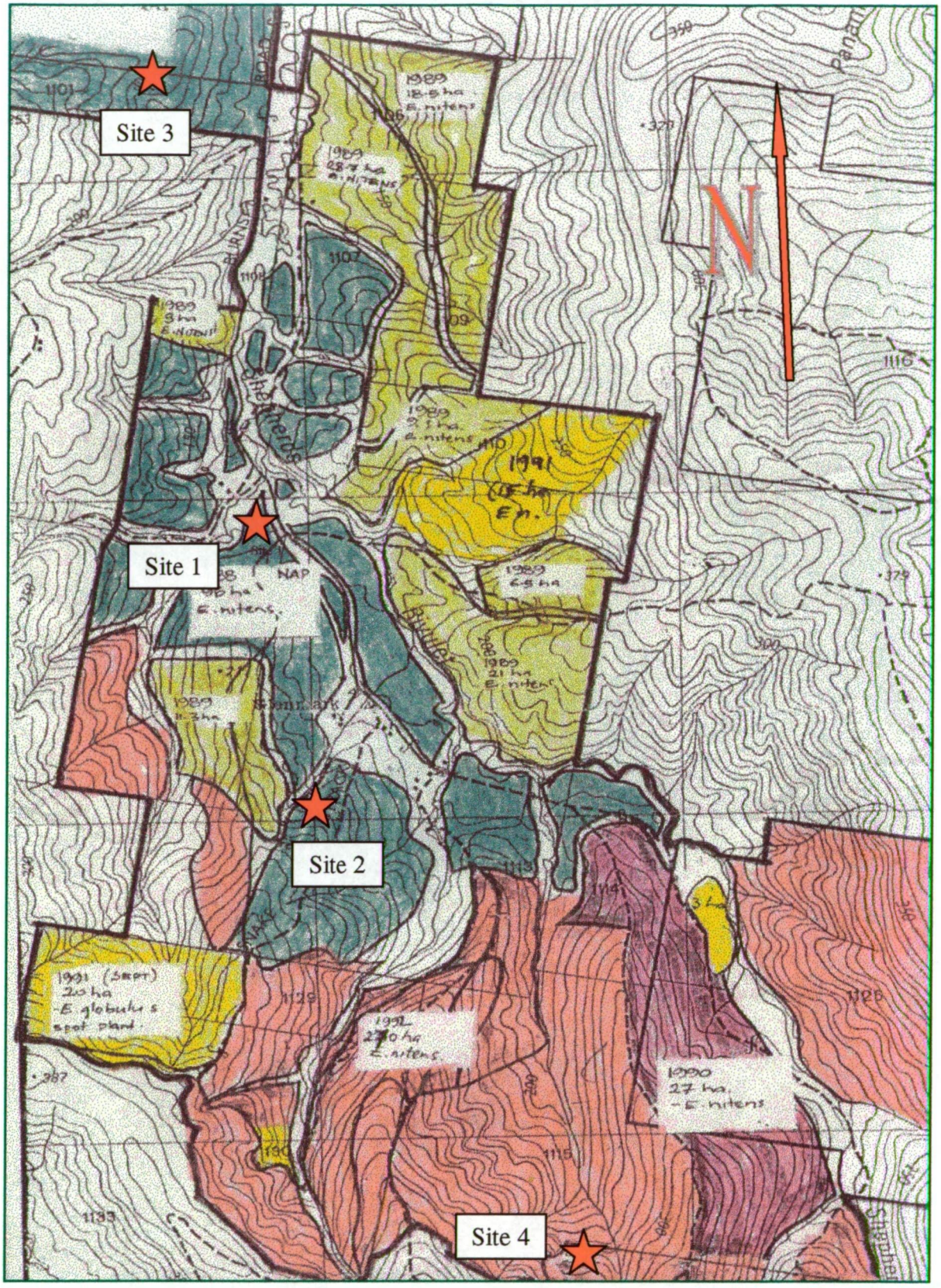


Figure 2.2 Location of the experimental sites at Wyena. Green shading represents 1988 planting, orange shading represents 1992 planting. Red stars indicate position of experimental sites 1 - 4.

Site 3 was located in a 1988 planting approximately 1 km fom Site 1, at a topographically similar location to that site near the base of an adjacent slope. The soil profile was shallower than at either Site 1or Site 2 and it had historically performed poorly from an agricultural perspective (Joe Jensen, pers. comm.). *A. dealbata* was present in varying density across Site 3 and was the only significant woody weed.

Site 4 was situated in a 1992 planting on an upper slope at the plantation's topographically highest point.

2.2.4 Growth plots

In April/May 1994, *A. dealbata* stem density was measured in 20 plots (108 m^2-192 m^2) at a range of locations across the plantation (representing variation in topography, site history, elevation and planting date) in order to identify suitable experimental and measurement sites.

Twenty-two plots were then established across the four sites. Nine plots (A-I) were established in August 1994 at Site 1 in a three by three square (Figure 2.3a). Each plot contained the area covered by sixteen eucalypts in a four by four pattern (a nominal area of 192 m^2). Nine similar plots were established in August 1995, five at Site 2 (J, K, L, M, N) (Figure 2.3b) and four at Site 3 (O, P, Q, R) (Figure 2.3c). Sites 1 and 3 were infested by high numbers of *A. dealbata*. *A. dealbata* competition was absent from Site 2. Four additional plots (S, T, U, V) were established at Site 4 (Figure 2.3d). Three of these (S,T,U) were established in September 1994 and represented respectively moderate, minimal and severe competition from *Acacia* (based on the degree of *A. dealbata* canopy cover). The canopy was closed for Plots U and V but not for Plots S and T. A closed canopy in this instance refers to where the crowns of *A. dealbata* and *E. nitens* formed a

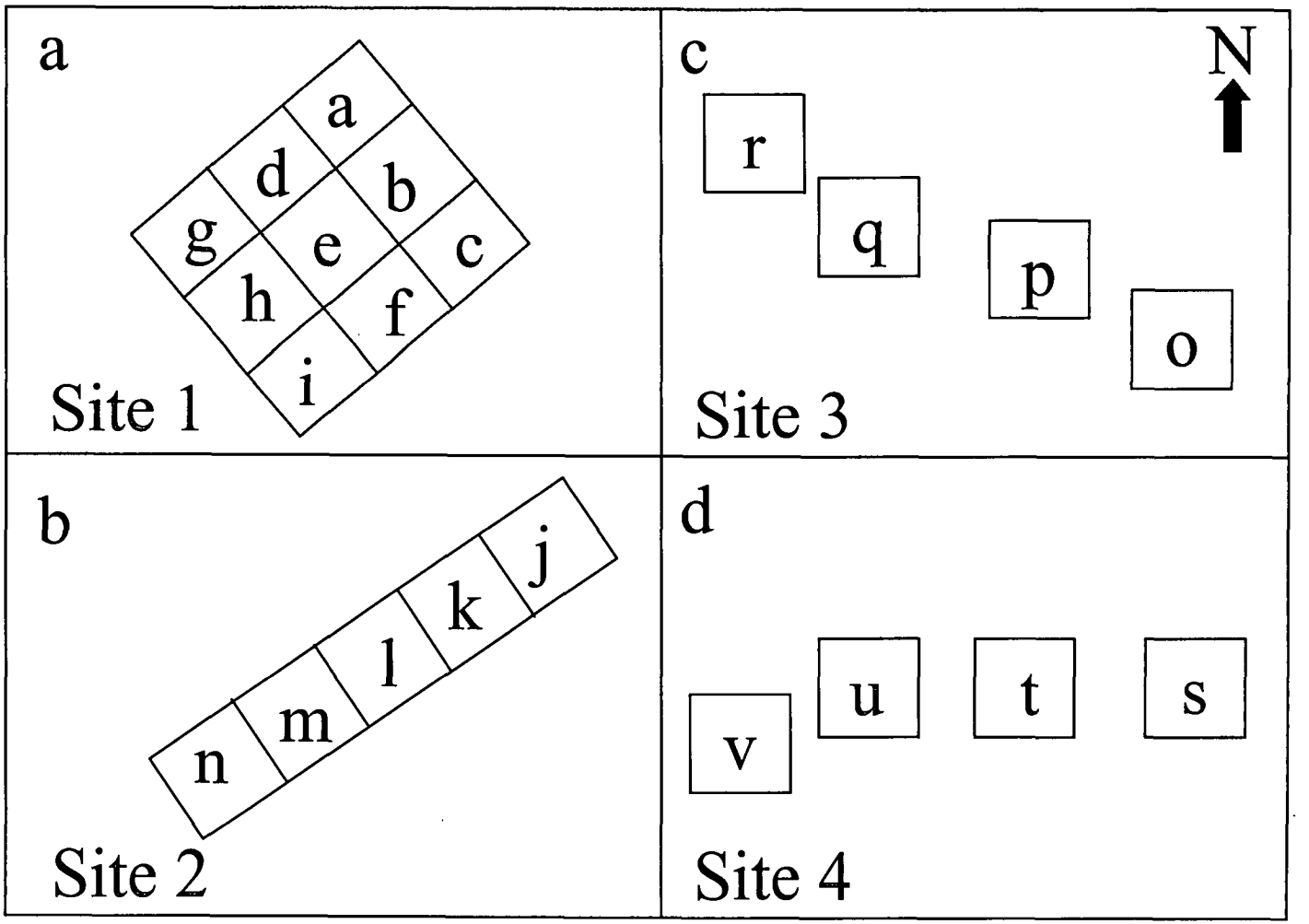


Figure 2.3 The layout of measurement plots at the four experimental sites described in Figure 2.2

continuous layer that left no room for horizontal growth of crowns (and thus a greater share of light capture) without competition with another stem occurring. Each plot (S, T, U) consisted of twelve trees in a three by four pattern covering a nominal area of 144 m^2. The fourth plot (V, of similar design) was established in September 1995 in an area of severe competition adjacent to Plot U above. There were at least four buffer rows between each plot and the edge of the stand and at least a single buffer row of trees separated adjacent plots at each site. Establishment characteristics of sites and plots are summarised in Table 2.1.

Table 2.1 Distribution of sites and growth plots used in the experiments

Site	No. Plots	Planting year	No. Trees	Area (m^2)	*Acacia* density	Plot Establishment
1	9 (A-I)	1988	16	192	High	Aug-94
2	5 (J-N)	1988	16	192	None	Aug-94
3	4 (O-R)	1988	16	192	High	Aug-94
4	3 (S-U)	1992	12	144	Range	Sep-94
4	1 (V)	1992	12	144	High	Sep-95

2.2.5 Ecological release experiment

A. dealbata was cleared from Plots Q and R in August 1995, and from Plots A, E and V in September 1995 in an ecological release experiment.

2.2.6 Tree measurement program

Diameter (d) at breast height (1.3 m above ground) over bark of eucalypts was measured using a diameter tape in August 1994 at Site 1, and in September 1995 and September 1996 at all sites. Total height (h_t) and height at base of live crown (h_c) were measured using a digital hypsometer ('Vertex', Forestor Instruments AB Sweden) on the latter two measurement dates at all sites. Tip height was also measured using height poles at Site 4 in September 1994. Diameter of *A. dealbata* was measured in August 1994 at Site 1 and at Sites 1, 3 and 4 in September 1996. Diameter of *A. dealbata* was not measured in 1995. Tip height of *A. dealbata* was measured using height poles at Site 4 in September 1994 and h_t and h_c were measured at all sites using the hypsometer in September 1996. In 1995, three eucalypts were removed from Plot D in a biomass experiment (see Chapter 3). Plots B, C, F, G, H and I were not modified. Height and diameter measurements of eucalypts were also made in March 1996 at Site 3 and in the plots used in the ecological release experiment. *A. dealbata* stem density was recorded for all plots at all measurement times.

A final measurement of diameter at breast height for eucalypts in plots A, B, C, E, F, G, H, O, P, Q, R, U and V was made in November 1997.

2.2.7 Soil analysis

In October 1996, soils were sampled for chemical analyses. Eighteen samples were taken from each of Sites 1, 2 and 4, and twelve samples from Site 3. Sample points were chosen in a pseudorandom manner to ensure that a minimum of 2 samples were taken per plot at each site. In all cases a 0.00045 m^3 volume of soil was removed from the top ten centimetres of the profile and frozen until analysis. Additionally, a soil pit was dug at Site 1 and a similar volume of soil was sampled at four depths in the profile. Samples were air dried, ground and sieved (<2 mm, <0.5 mm fractions) prior to analysis. Total nitrogen,

extractable phosphorus, exchangeable cations (Mg, Ca, K, Na), pH, electroconductivity (E_c), moisture content and loss of carbon on ignition (LOI-C) were all determined using standard methods (Rayment and Higginson 1992, methods 7A4, 9B1, 15A1, 4A1, 3A1, oven dried at 75°C [17 h] and furnaced at 375°C [17 h] respectively).

2.2.8 Data analysis

Basal areas were calculated for all measurement series. Stand volume was also calculated for those measurement times when heights were available (Opie et al., 1978). Data were analysed using linear regression and ANOVA (SAS Institute, Inc., 1990) and simple descriptive techniques.

2.3 Results

2.3.1 Density

In April/May 1994, *Acacia* density varied across the experimental site from 0 to 40 000 stems ha^{-1}. Areas of extremely dense *Acacia* populations (> 20 000 stems ha^{-1}) were restricted primarily to drainage lines, depressions and road/tracksides. However, very high *Acacia* densities (> 10 000 stems ha^{-1}) were found among all topographic positions in the initial survey. *Acacia* was absent from some locations (eg Site 2, Table 2.2) where aspect and slope were identical to those where heavily infested plots occurred. Soils were not found to be physically distinct between such sites. Frequencies greater than 10 000 stems ha^{-1} were recorded only at sites planted after 1990 or areas that had been disturbed after this date. Density of *A. dealbata* decreased significantly ($p<0.05$, t-test) at Site 1 during the study period, remained steady in the severely competing 1992 plot (Plot U) but almost doubled in the moderately competing 1992 plot (Plot S), predominantly through root

suckering (Table 2.2). Even though *A. dealbata* stem density was high in Plot S, stems were small and restricted predominantly to mounds. This was in contrast to the spatially homogeneous stem distribution recorded at Plot U. *A. dealbata* stem density was found to be significantly and inversely related to *E. nitens* basal area both among plots at Site 1 at age 6 years (Figure 2.4a) and across the plantation generally at age 8 years (Figure 2.4b).

2.3.2 Basal area

Total plot basal area of *A. dealbata* and *E. nitens* varied significantly within Site 1 for both 1994 and 1996 measurements. The *Acacia* plot basal area appeared to decrease with distance upslope but this could not be demonstrated statistically. The relationship between *E. nitens* and *A. dealbata* plot basal area could not be described by a significant regression equation for either data set (Figures 2.4c & 2.4d). There was no significant difference in *E. nitens* total basal area among plots at Site 2 ($p>0.5$). There was a significant difference in *E. nitens* total basal area between Site 1 and Site 2 ($p<0.05$) but no significant difference ($p>0.05$) between total (tree) basal area at the two sites. Repeated measures analysis of changes in total basal area over time at Sites 1 and 2 indicated a significant effect of treatment (*Acacia* presence or absence - $p<0.05$) but no significant time*treatment effect ($p>0.05$). At Site 4, few statistical analyses were possible due to the lack of plot replication (precluded by site heterogeneity). Regression analysis yielded a significant relationship ($p<0.05$) between eucalypt and *Acacia* basal area over the three plots (S, T, U) for 1996 data ($y = -0.19x + 8.43$) but not for 1994 data. Visual assessment of differences in growth among the plots (Figure 2.5) indicated that differences among treatments were increasing over time.

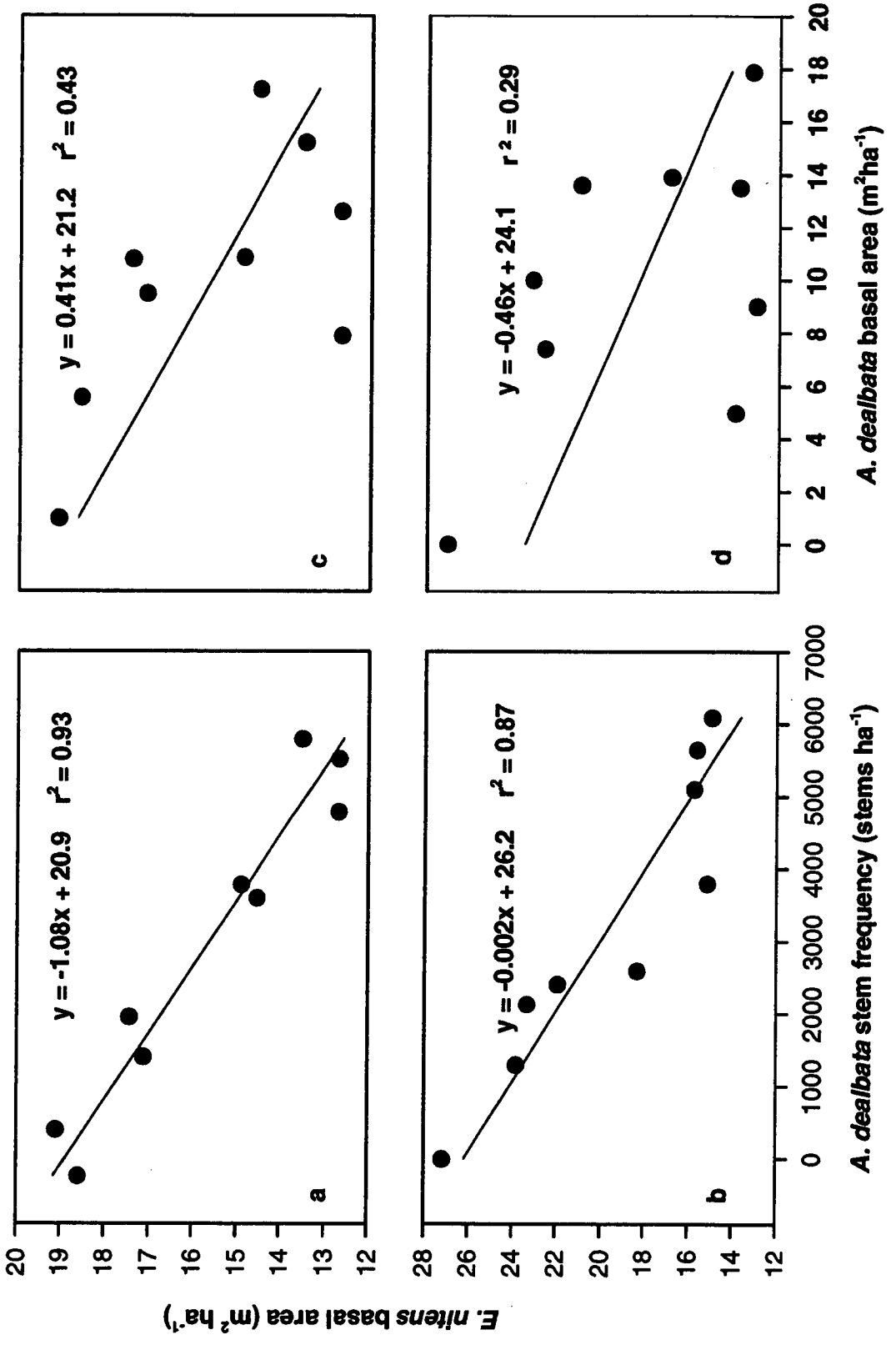


Figure 2.4 The relationship between *A. dealbata* stem density and *E. nitens* basal area in (a) August 1994 (age 6 years) and (b) September 1996 (age 8 years); and the relationship between *A. dealbata* basal area and *E. nitens* basal area in (c) August 1994 and in (d) September 1996. In 1994 all 9 plots at Site 1 were considered. In 1996, data from the eight unmodified plots at Sites 1 and 3 were used. The mean of Site 2 plots was used to provide an appropriate acacia-free reference for the 1996 analyses.

Table 2.2. Plot biometric characteristics in September 1996

(Site 1, A-I; Site 2, J-N; Site 3, O-R; Site 4, S-V).

Plot ID	*A. dealbata* frequency (stems/ha)	*E. nitens* basal area m^2ha^{-1}	*A. dealbata* basal area m^2ha^{-1}	Total plot basal area m^2ha^{-1}	*E. nitens* vol m^3ha^{-1}	*E. nitens* MAI $m^3ha^{-1}a^{-1}$
A*	0	19.3	0.0	19.3	203.7	25.5
B	2407	21.9	13.6	35.5	228.0	28.5
C	1296	23.8	10.0	33.8	258.9	32.4
D*	0	13.5	0.0	13.5	147.4	18.4
E*	0	18.0	0.0	18.0	191.4	23.9
F	2130	23.3	7.4	30.7	256.8	32.1
G	5648	15.6	13.5	29.1	165.8	20.7
H	3796	15.1	17.9	33.0	162.1	20.3
I	2593	18.3	13.9	32.2	229.6	28.7
J	0	31.4	0.0	31.4	320.1	40.0
K	0	21.6	0.0	21.6	212.8	26.6
L	0	21.7	0.0	21.7	251.8	31.5
M	0	33.0	0.0	33.0	326.8	40.9
N	0	28.0	0.0	28.0	285.4	35.7
O	5104	15.7	5.0	20.7	185.1	23.1
P	6094	14.9	9.0	23.9	168.9	21.1
Q*	0	9.9	0.0	9.9	110.6	13.8
R*	0	14.0	0.0	14.0	99.9	12.5
S	20278	6.8	4.8	11.6	91.0	22.7
T	0	9.0	0.0	9.0	139.0	34.8
U	14444	4.0	24.0	28.0	59.7	14.9
V*	0	5.9	0.0	5.9	85.4	21.4

* Plots have been modified

At Sites 1 & 3, the proportional basal area growth of eucalypts in plots cleared of *Acacia* (A, E, and Q, R respectively) was not significantly different from that in plots with continuing *Acacia* competition two years after treatment (repeated measures analysis). At Site 4, after one and after two years, the mean proportional basal area growth of the released eucalypts (Plot V) was higher than that of the controls (U).

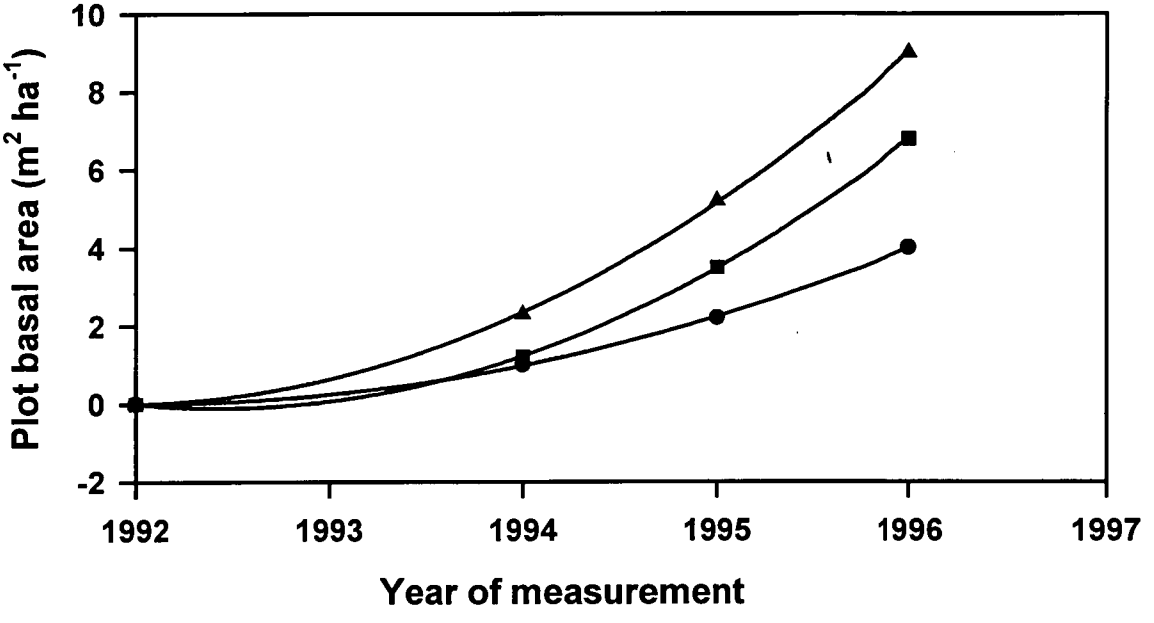


Figure 2.5 Changes in *E. nitens* basal area over time in three 4-year-old plots representing varying levels of competition from *A. dealbata* (S, T, U - respectively moderate, minimal and severe competition). Regression lines are all significant ($p<0.05$). Refer to Tables 1 and 2 for plot descriptions.

2.3.3 Distribution

The frequency distribution of diameter classes of *A. dealbata* indicated similar patterns in 1994 and 1996 but differed among plots/sites (Figure 2.6). The histogram for Plot S indicated high but waning recruitment whereas Plot U comprised a more even distribution

with low recruitment (if any). At Site 1, recruitment of new stems appeared not to occur during the measurement period and many small moribund stems were suppressed and died. Plot replication was insufficient to allow statistical analysis of differences in distribution modifying functions (*sensu* Westoby 1982).

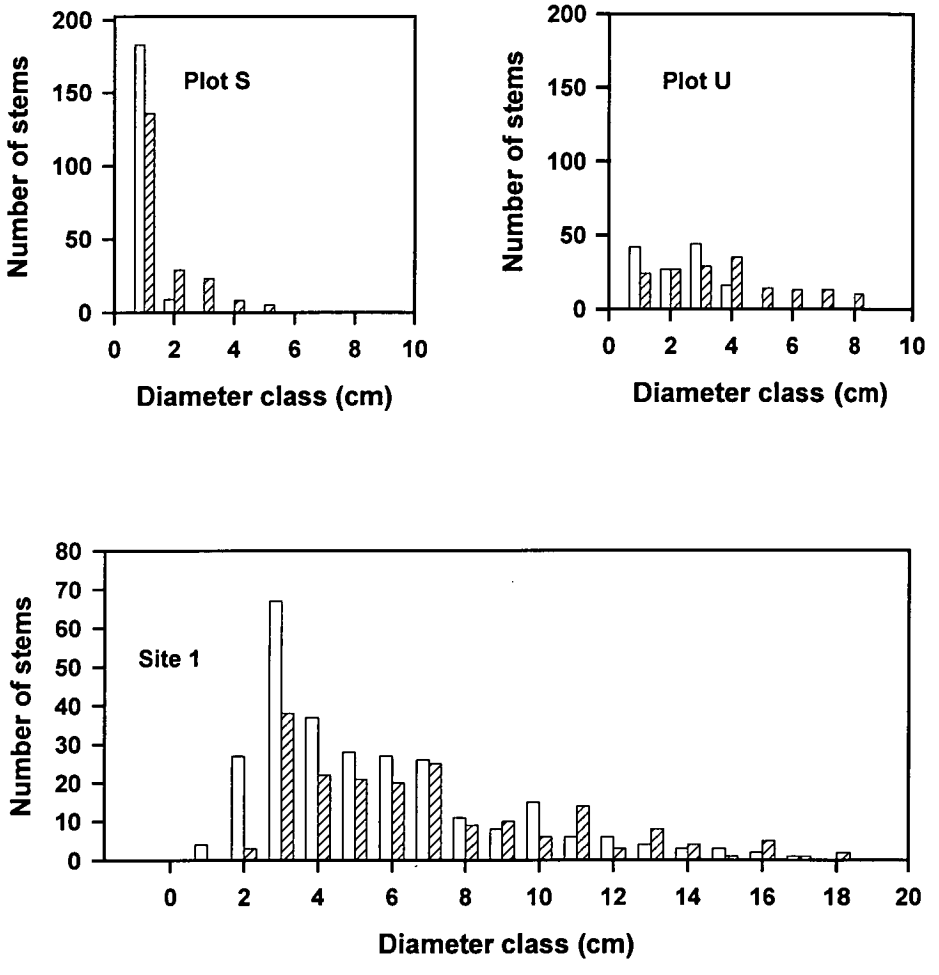


Figure 2.6 Population histograms for *A. dealbata* in Plots S and U at Site 4, (2.6a) and (2.6b), and for Site 1 plots combined (2.6c).

2.3.4 Soil

Application of t-tests (two sample assuming equal variances) to soil data from Site 1 plots and Site 2 plots (*A. dealbata* presence and absence respectively) yielded significant differences ($p<0.05$) in N, Ca, K and very highly significant differences ($p<0.001$) in pH, E_c, moisture, LOI-C and Na. At Site 4, there were significant differences between Plots U and T in P and Ca ($p<0.05$), moisture, LOI and K ($p<0.01$) and N ($p<0.001$) (Table 2.3). A further significant difference in soil moisture was recorded between Plot U and Plot S ($p<0.01$). Linear regression did not significantly describe relationships among soil variables and *Acacia* basal area for 1988 or 1992 plots (except for a significant result for Mg in 1988 planting). For 1988 plots, there was a significantly higher moisture content in soils with *A. dealbata* presence than without ($p<0.01$; *t*-test, two tailed). When data were pooled for 1988 and 1992 plots, a significant positive regression was yielded for the relationship between soil moisture and *Acacia* basal area ($y = 0.06x + 0.82$, $r^2 = 0.79$, $p<0.01$).

Table 2.3. Soil characteristics of experimental plots. For sites and year of establishment, see Table 2.1.

Plot ID	pH	E_C dSm^{-1}	Moisture %	LOI-C %	N %	P $mg\ kg^{-1}$	Ca $mg\ kg^{-1}$	Mg $mg\ kg^{-1}$	K $mg\ kg^{-1}$	Na $mg\ kg^{-1}$
A	4.40	0.14	1.81	11.10	0.39	46.25	984.60	146.26	152.16	17.09
B	4.41	0.13	1.73	11.37	0.29	40.45	776.31	120.88	175.92	10.32
C	4.87	0.11	1.40	8.99	0.35	31.97	1031.32	168.60	190.29	14.99
D	4.31	0.16	2.28	15.99	0.73	105.14	824.60	121.14	237.42	8.59
E	4.50	0.09	1.21	7.44	0.46	37.31	584.61	87.89	145.28	4.64
F	4.78	0.10	1.33	9.42	0.43	31.10	914.69	165.77	161.81	6.61
G	4.78	0.14	1.27	8.34	0.30	23.87	857.96	148.11	200.33	8.98
H	4.66	0.11	1.86	8.59	0.44	30.97	820.33	124.64	161.94	6.08
I	4.70	0.08	1.44	7.60	0.43	30.62	704.81	118.26	120.21	8.68
J	4.75	0.09	0.94	6.00	0.33	49.07	714.03	190.60	221.71	41.92
K	4.90	0.08	1.38	7.42	0.36	49.24	1032.29	143.27	135.39	39.32
L	5.12	0.08	1.17	6.84	0.33	41.74	1223.16	147.91	112.99	47.26
M	5.00	0.07	1.15	7.29	0.35	37.43	966.11	127.86	103.46	39.34
N	5.02	0.08	1.20	7.34	0.31	29.08	1106.98	156.73	129.74	31.75
O	4.56	0.12	1.49	8.70	0.29	24.38	520.08	138.55	166.80	7.22
P	4.43	0.13	1.34	8.76	0.32	24.74	375.67	126.97	152.62	29.27
Q	4.43	0.16	2.04	10.21	0.44	39.25	956.06	156.76	158.65	20.96
R	4.27	0.15	1.67	10.52	0.50	22.47	632.49	160.65	137.03	30.50
S	5.18	0.07	1.04	4.91	0.21	12.80	637.38	239.33	159.54	33.63
T	5.17	0.10	1.33	6.85	0.25	21.46	674.81	252.33	244.53	39.46
U	5.16	0.14	2.40	13.81	0.68	40.31	2292.18	391.52	441.22	55.53
Data summary, 1988 planting (Plots A - R).										
Acacia-infested (n=12)*	4.57	0.12	1.55	9.25	0.39	31.95	763.25	138.61	160.25	13.78
Acacia-free (n=5)	4.96	0.08	1.17	6.98	0.34	41.31	1008.51	153.27	140.66	39.92

* Plot D data excluded due to plot modification by destructive sampling

2.4 Discussion

This study has demonstrated that competition from *A. dealbata* regeneration may have a significant negative effect on the early growth of *E. nitens* in a young plantation. The degree of infestation by *A. dealbata* was associated with decreases in *E. nitens* basal area from age 2 to 8 years. However, patterns of competition appeared strongest between age 2 and 5 years, prior to suppression (change from co-dominance to sub-dominance with respect to *E. nitens*) of the *A. dealbata* canopy.

The distribution of *A. dealbata* in the plantation was controlled by several contributing factors. The importance of a suitable seed bed was indicated by *A. dealbata* favouring mounds in some plots (eg Plot S). However, this occurred only in areas where very shallow soil profiles existed. These were the ex-native forest sites where erosion had been considerable during plantation establishment. On the ex-agricultural sites, where soils were uniformly deeper and better developed, the presence of the seed itself in the soil was of greater importance. This was linked to the presence of mature acacias in the pre-agricultural native forest and in turn to microclimatic factors controlling their distribution. Thus drainage lines, gullies and lower slopes were very favourable for seed deposition and retention. Those sites where *A. dealbata* growth was most prolific were dominated by mature acacias prior to clearing for agriculture (Joe Jensen, former landholder, pers. comm.).

Patterns of site burning strongly influenced the development of *A. dealbata* populations where seed was present in the soil. *A. dealbata* has been shown to germinate better after slow high intensity fires whereas *Pomaderris* spp (for example) germinate more prolifically after fast low intensity fires (Cunningham and Cremer 1965). At the study site,

A. dealbata was more prevalent in areas of ex-native forest that received higher intensity fires at establishment, whereas ridges and the margins of the plantation were dominated by *Pomaderris* growth. The use of fire in manipulating weed regeneration at such sites, in terms of both species and abundance, has previously been mooted by Floyd (1966). Importantly, Floyd noted that when mechanical land clearing methods were used at a wet eucalypt site, innocuous annual weeds constituted 78% of subsequent non-crop production. At a corresponding burnt site, 75% of production was contributed by potentially harmful weeds - woody species or those with established root systems.

In areas where *A. dealbata* germinated in large numbers, the timing of herbicide application strongly influenced their growth. At Site 2, herbicide was not applied until six months after other site preparation was completed. Consequently, herbicide was applied to *A. dealbata* regrowth rather than to bare soil. At an adjacent site considered in initial 1994 density measurements (a 1988 planting), *A. dealbata* was present in insignificant numbers (density of 5-10 stems per hectare) and at best attained a subdominant canopy position. Whilst the exact timing of herbicide applications at the study site was not recorded, Milton and Moll (1982) contend that Australian acacias are best controlled by herbicide applications in autumn or winter. The assertion is supported by Flinn and Hopmans (1977) who reported successful control of *A. dealbata* in Victoria by a single winter herbicide application.

Regression relationships developed in Figures 2.3a and 2.3b demonstrated the capacity for *A. dealbata* to effectively compete with the plantation eucalypts. Competitive interactions between *A. dealbata* and both eucalypts and *Pinus radiata* D. Don have long been recognised (Elliott 1978) and the ability of *Acacia* spp to depress the growth of plantation

P. radiata has been demonstrated elsewhere (Turvey et al. 1984). In the latter study, both *Acacia* basal area and stem density were correlated with decreased pine stem volume with a 50% loss of potential pine volume being attributed to a stocking density of 400 - 500 *Acacia* stems ha^{-1}. In the present study, a similar reduction in *E. nitens* volume was recorded in the 1992 planting, although the figure was less than half this in the 1988 planting (based on 1996 data).

Whilst differences in eucalypt total basal area were measured between infested and non-infested sites of both planting dates (1988 and 1992), significant regression relationships between *A. dealbata* basal area and eucalypt basal area could only be developed in the 1992 stand. Root suckering by *A. dealbata* in Plot S precluded the development of a significant relationship between *A. dealbata* stem density and *E. nitens* basal area in the 1992 stand. In older stands, stem density of *A. dealbata* was more sensitive than basal area in reflecting changes in competition as stems can remain viable but moribund without significant diameter growth for long periods. This indicates that patterns of competition were probably established in the early stages of the plantation but that they are harder to define subsequently. The histograms of population structure for the two age classes (Figure 2.5) support this assertion. It is difficult to differentiate between newly recruited/actively growing stems and those that are barely surviving (moribund) based on frequency distribution of diameter data alone. Plot S had not reached canopy closure at 4 years and light was plentiful at the ground whereas in Plot U, canopy closure had occurred by age two. Whilst eucalypt crowns in Plot S were larger (higher mean green crown length), the additional presence of comparatively large *A. dealbata* crowns in Plot U resulted in heavy shade at the ground. It is likely that early establishment of acacias is strongly controlled by light. In addition, the significantly higher moisture content in Plot U than Plot S suggests

that following *Acacia* establishment it is both water and light that limit the success of acacias in attaining growth rates similar to eucalypts. Notably, acacias were evenly distributed about Plot U whereas they were restricted predominantly to mounds rather than inter-rows in Plot S. The importance of soil moisture for early *A. dealbata* growth is further supported by the significant association between *A. dealbata* basal area and soil moisture reported in the results.

The results of ecological release of plantation eucalypts from *A. dealbata* competition indicate that competition is waning in older stands. Growth of released trees from the older stands (released at age 7) was not significantly greater than controls. It follows that whilst competition may still exist at age eight years it is not as intense as earlier in the rotation.

Soil nitrogen has been increased by up to 28% in pine stands with heavy *A. dealbata* growth, but with no improved pine growth resulting (Turvey et al. 1984). In the present study, soil nitrogen in the 4-year-old *Acacia*-infested plot (Plot U) was more than double that in the corresponding *Acacia*-free plot (Plot T). Whilst differences in the older plots were not as large, they were nevertheless significant. At both ages, the greater abundance of nitrogen did not evoke an increased growth response in the plantation species but rather was associated with reduced productivity of the eucalypt. It is therefore evident that competition for light and/or water occurs between the two species. This competition is maximised at canopy closure and declines. Although the reasons for the decline in competitive success of *A. dealbata* are likely to include interspecific differences in physiological behaviour and resource allocation, heavy intraspecific competition within *A. dealbata* is indicated by the population data (Figure 2.5). Temporal changes in stand distribution of stem diameter result from variation in growth rate and mortality rate and have been studied in both pure stands (eg Westoby 1982) and mixed even aged stands

(Shainsky and Radosevich 1992; Bi and Turvey 1996). These changes are generally attributed to competition for light (eg Larocque and Marshall 1993). Thus, in this study, a high density of *A. dealbata* will have led to greater intraspecific and interspecific competition for light. Increases in mean height:diameter ratios result in smaller stems, which are sensitive to competition, being eliminated from the population. As acacias are characterised by more slender stems than the eucalypts, it is these rather than the eucalypts that eventually will be eliminated by interspecific competition. It is notable that competition for light has been shown to reduce drought resistance of seedlings due to decreases in root/shoot ratios for both *Acacia* and *Eucalyptus* species (Withers 1979) (see Chapter 4 and Chapter 7 for a more detailed discussion). Therefore, whilst the primary limiting resource in mixed stands is light, a secondary effect of water limitation may be indicated for stands with very dense *A. dealbata* populations. In the following chapters, the mechanisms and extent of competition for these two resources will be examined.

Chapter 3. Canopy structure and architecture 1: Specific leaf area and the relationship between stem variables and leaf area

3.1 Introduction

Results reported in Chapter 2 indicated that competition for light was occurring in mixed stands of *E. nitens/A. dealbata* of both ages. It is therefore necessary to consider the magnitude and spatial arrangement of the contribution of *A. dealbata* to stand leaf area. Descriptions of canopy architecture have been used for the characterisation of patterns of stand production (McCrady and Jokela 1996), water use (Grier and Running 1977), interception of radiation (Linder 1985) and precipitation (Dufrene and Breda 1995), and turbulent transport (Jarvis and Leverenz 1983). Hence, in the context of this study, such a description may facilitate an understanding of stand distribution of both light (energy) and water (see Chapter 6).

In studies of this kind, the temporal and spatial distribution of leaves is the most important canopy architectural variable to consider and leaf area index (LAI) is the most commonly integrated mathematical form of this distribution (Landsberg 1986). In terms of radiation distribution within the canopy, non-foliar components of tree crowns may become important. For this reason, both plant area index (PAI *sensu* Gazarini et al. 1990) and vegetation area index (VAI *sensu* Fassnacht et al. 1994) have been put forward as alternative structural descriptors. Relationships between LAI and productivity (eg Vose and Allen 1988) and LAI and evapotranspiration (eg Swank et al. 1988) are well established: however the relative merits of the various methods available for measurement of LAI are less clear.

LAI may be measured either directly or indirectly. Direct measurements may be destructive, relying on leaf sampling. Such an approach is labour intensive, time consuming and has been described by Welles and Norman (1991) as "nearly impossible in large forest canopies", primarily due to logistical difficulties in the adequate characterisation of foliage distribution (Smith et al. 1993). A variety of destructive methods has been developed including the stratified clip method, the dispersed individual plant method and the litterfall collection method (Norman and Campbell 1989). Non-destructive direct methods include the point quadrat method (Warren-Wilson 1960), the use of fisheye photographs (Anderson 1970) and the use of digital videography (eg Law 1995).

Indirect methods consider the relationship between the radiation environment below or within the tree canopy, and the leaf area of the canopy. Mathematical techniques based on gap fraction measurements include the direct inversion method (eg Perry et al. 1988) and the bisection method (Campbell and Norman 1989). Indirect methods overcome many of the logistical problems of direct methods, but require calibrations which have been shown to be no more portable than relationships derived from direct approaches. The above measurement and associated instrumentation have received recent review in the literature (Campbell and Norman 1989; Goel and Norman 1990).

A common method for estimating leaf area at the stand scale uses a combination approach. Destructive sampling of trees is used to develop allometric relationships between leaf area (or leaf mass) and a related stem variable (e.g. basal area or sapwood area) for each canopy element that is being examined (ie species, size classes or crown layers). The allometric relationships are then used in combination with tree basal area (or sapwood area determined by cores) to scale up to the stand level (eg White 1996). Furthermore, by using subsampling procedures (Pinkard and Beadle, 1998) to describe linear relationships

between branch cross-sectional area and branch leaf area (Webb and Ungs 1993), the destructive sampling involved in developing the above relationships for a given site may be reduced to a manageable level.

Sapwood area is the functional variable likely to be most highly correlated with leaf area (Waring et al. 1982) and accordingly the most common stem variable used for scaling. However, the nature of that relationship is not clear and its acceptance is not universal (Pereira et al. 1987). Whilst leaf area is normally considered to be a function of sapwood area (as interpreted by the pipe model *sensu* Shinozaki et al. 1964), some studies have indicated that sapwood production in fact may be dependent on foliage area (eg Kaufmann and Troendle 1981). Regardless of the direction of causation, the relationship between sapwood area and leaf area is at least functional, and thus should be portable (Lavigne et al. 1996).

Even so, such relationships are not universal (Gazarini et al. 1990) and have been shown to vary with species (Kaufmann and Troendle 1981) and a range of site and stand variables (Brix and Mitchell 1983, Espinosa Bancalari et al. 1987, Keane and Weetman 1987, Grier and Running 1977, Mencuccini and Grace 1995). Cross-sectional sapwood area tapers from breast height to the crown base, partly due to the increase in sapwood allocation to storage with distance from crown break (Hillis 1987). Therefore, measurement at the base of the crown should facilitate derivation of a closer relationship with leaf area than measurements from lower in the stem (Maguire and Batista 1996). Such a measure is often impractical on a large scale, particularly where crown lift is marked. However, sapwood taper is a non-linear function of crown height (Maguire and Hann 1990, Medhurst et al. in prep). Thus, variation in the degree of taper between sites (influenced by site and silvicultural factors) may be accounted for in development of allometric relationships by

the use of both sapwood area and crown height for their derivation (Medhurst et al. in prep). These relationships will then be inherently more portable.

For allometric relationships that are developed for local scaling exercises rather than for wider modelling purposes, portability is less important and the utility of a stem scaler is enhanced by its ease of measurement. The measurement of sapwood area may be difficult and this is particularly the case in stands where axial or radial distribution of sapwood is uneven (see Chapter 6). In such cases, stem core sampling must be replaced by destructive sampling of trees and the subsequent use of the relationship in scaling exercises is precluded (as it is generally impractical to destructively sample all trees in a stand). Furthermore, the difficulty in delineating functional from non-functional sapwood may cause bias in the measurement. Under such circumstances, basal area may be the most appropriate measurement with which to develop stem variable:leaf area allometric relationships.

The objective of this experiment was to determine the relationships between leaf area and a number of stem variables for both *E. nitens* and *A. dealbata*. Thus, the most appropriate scaling variable could be identified and a three-dimensional description of canopies be permitted (see Chapter 4). Furthermore, species and treatment differences in the functional relationship between sapwood area and leaf area may be useful in identifying the physiological processes underlying competitive success or failure, particularly in combination with water relations and gas exchange data (see Chapter 7). This experiment therefore tests the hypotheses that:

1. as sapwood area is functionally related to leaf area, it is the most appropriate stem variable to use in scaling tree leaf area to stand leaf area and

2. relationships between sapwood area and leaf area are stable across the treatments considered.

Trees in *Acacia*-infested stands and *Acacia*-free eucalypt stands of two ages were considered.

As determination of specific leaf area is a prerequisite for estimation of tree leaf area, the relevant data are reported and discussed in this chapter.

3.2 Materials and methods

Three sites were used for experimentation, Sites 1 and 2 in the 1988-planted coupe on ex-agricultural land and Site 4 in the 1992-planted coupe on cleared native forest. At Site 4, the stem density of *A. dealbata* was highly variable, enabling sampling at both *Acacia*-free and *Acacia*-infested locations (Plots T and U respectively). Site 1 experienced a very high density of *A. dealbata* stems whereas Site 2 was *Acacia*-free. (Refer to Chapter 2 for detailed site and plot descriptions.)

3.2.1 Sampling procedure

1995

In July/August, eucalypts at Site 1 were divided into three size classes based on diameter at breast height (*d*). A single tree, representative of each class, was sampled. Acacias at Site 1 were divided into three classes on the basis of canopy position. Three co-dominant, three subdominant and six understorey trees were felled and sampled in the same manner as above. The trees in each *Acacia* class were chosen to represent the variation in diameter of that class. A further three eucalypts were sampled at Site 2. Selection procedure was identical to that for eucalypts at Site 1.

Total height (h_t) and height to the base of the live crown (h_c) were measured for each tree as were d and diameter at the base of the crown. Total crown dimensions were measured (see Chapter 4) prior to the crowns being divided vertically into thirds based on a simple horizontal division of the crown length (Figure 3.1). Leaves were separated for each crown third for dry weight analysis and leaf area measurement. All foliage was air dried to constant weight at 40°C (W_{40}) prior to oven-drying subsamples to constant weight at 80°C (W_{80}). The ratio W_{80}/W_{40} was used to convert the bulk leaf weights to oven-dry equivalents. This was done because of the logistical difficulties associated with oven-drying entire crowns of large trees.

At Site 4, three acacias and three eucalypts in Plot U and three eucalypts from Plot T were selected as above and sampled for tree and crown dimensions and specific leaf area.

1996

In July/August, 5 eucalypts and 5 co-dominant acacias at Site 1 were selected to represent the variation in diameter present at the site. Each tree was felled at ground level with a chainsaw. d was measured for each tree as were h_t and h_c, yielding green crown length (l_c). The height above ground and diameter over bark at 4 cm from the base of each branch were measured for each live branch from the base to the tip of the live crown. The crown was divided into thirds based on the origins of branches at the stem (Figure 3.1). On the basis of diameter distribution within each third of the crown, five representative branches were selected. Selected branches were excised at the base and removed to the laboratory for processing. Branch diameters were converted to cross-sectional area (csa) for the determination of regression relationships between branch csa, branch length and leaf area per branch which could then be used to estimate leaf area for whole crowns. Foliage was oven-dried to constant weight at 80°C (W_{80}). Additionally, five eucalypts and five acacias

were sampled from Plot U at Site 4 and a further five eucalypts were sampled from Plot T (as for 1995).

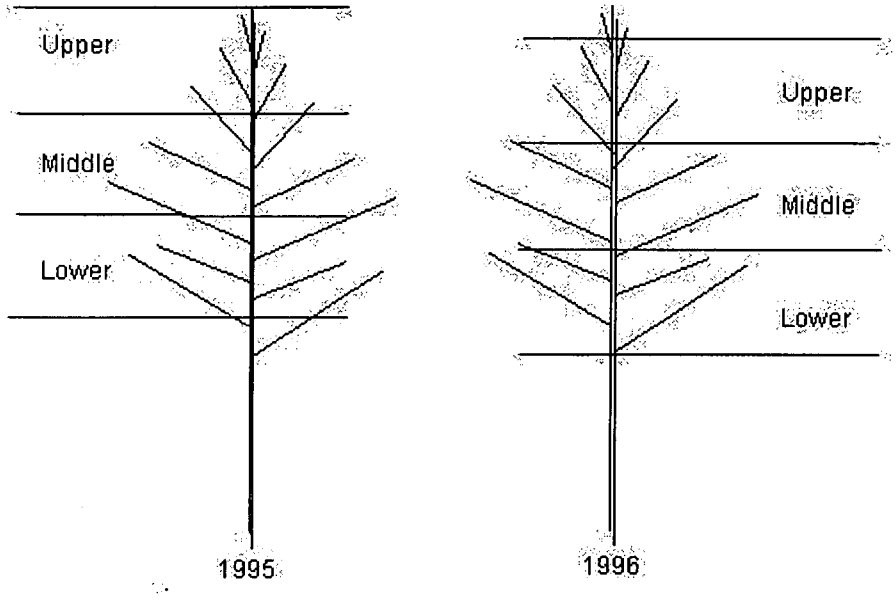


Figure 3.1 Division of crown zones for 1995 and 1996 sampling. In 1995, division was planar and based on foliar distribution. In 1996 division was based on inception of branches at the stem.

3.3.2 Leaf area determination

A subsample of leaves was used for the determination of specific leaf area (SLA). In 1995, 25 leaves were selected randomly from each crown third of each tree. In 1996, ten leaves were selected randomly from each sample branch. SLA was calculated on a projected leaf area or single-sided basis. Leaves were weighed fresh (W_f) prior to area determination (using a Delta-T leaf area meter in 1995 and using a flat-bed scanner and image analysis software in 1996 - see Chapter 5 for full description of image analysis of intact *A. dealbata* leaves) and oven-drying to W_{80}. Tree leaf area was calculated as the product of total leaf dry weight and SLA.

3.2.3 Sapwood area determination

Sapwood area was determined for breast height (1.3m) and crown base. This was achieved by staining the relevant stem disks with dimethyl yellow, tracing a stencil of the sapwood indicated by the stain and scanning the stencil for image analysis (as above).

3.2.5 Analysis

Linear regression was used to develop relationships between leaf area and stem variables. ANOVA and t-tests were used to investigate differences in SLA among treatments and crown zones. For relationships between basal area and leaf area and between sapwood area (at crown base) and leaf area, a residual sum of squares approach was used to investigate the significance of species, age and competition effects.

3.3 Results

3.3.1 Specific leaf area

Estimates of SLA of *A. dealbata* from 1995 were compromised by poorly repeatable leaf area measurements being returned by the leaf area meter. Leaves from 1992-planted stands were subsequently re-measured using digital image analysis, thereby obtaining satisfactory values. However, leaves from 1988-planted stands had deteriorated too greatly for re-measurement. Consequently, the accuracy of SLA data and of resultant calculations of tree leaf area of *A. dealbata* in 1988-planted stands was reduced.

In 1995, mean SLA varied from 48 - 86 $cm^2 g^{-1}$ for *E. nitens* and between 54 and 78 $cm^2 g^{-1}$ for *A. dealbata* (Table 3.1). For 1988-planted stands, there was no significant difference in SLA between *E. nitens* at Sites 1 and 2 (i.e. in the presence or absence of *A. dealbata*). However, in the 1992-planted stands, SLA was significantly higher for eucalypts in the *Acacia*-infested plot (Site 4, Plot U) than in the *Acacia*-free plot (Site 4, Plot T) ($p < 0.05$;

t-test). Combining Sites 1 and 2, and Plots U and T (to consider age effects), SLA was significantly lower in the 1988-planted stands). However, SLA of *A. dealbata* did not differ significantly between stands of the two ages (Site 1 and Site 4/Plot U).

Table 3.1. Mean specific leaf area ($cm^2\ g^{-1}$) for upper, middle and lower crown thirds by species, treatment and age in 1995 and 1996.

			Upper crown		Middle crown		Lower crown	
Species	**Planting date**	**Site/Plot**	**1995**	**1996**	**1995**	**1996**	**1995**	**1996**
E. nitens	1988	1	49	67	50	60	52	65
	1988	2	48	n.a.	52	n.a.	60	n.a.
	1992	4/U	56	57	73	64	86	71
	1992	4/T	48	59	66	64	68	75
A. dealbata	1988	1	54	48	62	51	78	69
	1992	4/U	58	50	58	55	73	64

n.a. Not available

Fewer trends were evident in the 1996 data set. Variation in SLA was smaller for both species (57 - 75 cm g^{-1} for *E. nitens* and 48 - 69 cm g^{-1} for *A. dealbata*) and differences between ages within each species were not significant ($p > 0.05$; t-tests). Neither was SLA significantly different between eucalypts growing in the presence or absence of *A. dealbata* (Plots U and T, Site 4).

SLA of *E. nitens* was lower than *A. dealbata* for the 1995 measure of Site 1 trees. However, in the following measurement year this trend was reversed. Eucalypts from the

younger stand (Site 4, Plot U) exhibited higher SLA than associated *A. dealbata* in both measurement years.

SLA almost invariably increased with crown depth (i.e. for upper crown foliage to lower crown foliage) for trees of both species, in stands of both ages and in each measurement year. Foliage of *E. nitens* at Site 1, 1996 measure, was an exception to this trend.

3.3.2 Leaf area vs sapwood area/basal area

1995 data

Tree leaf area was significantly related to sapwood area at breast height for both *A. dealbata* and *E. nitens* (Figure 3.2a). However, for acacias the relationship was better described by a second-order than a first-order regression (r^2 = 0.93 and 0.90 respectively). Of the acacias sampled only those in dominant canopy positions possessed crowns of similar sizes to eucalypts, subdominant and understorey trees contributing little leaf area to the mixed canopy. Eucalypts at Site 1 possessed smaller crowns than those at Site 2. At Site 1, eucalypt crowns possessed a significantly ($p < 0.01$) larger leaf area than acacias of the same sapwood area at that site (though species overlap occurred only at a sapwood area of about 100 cm^2).

For *E. nitens*, when basal area was related to leaf area (Figure 3.2b), the r^2 value for the first-order relationship was higher than when sapwood area was related to leaf area (Figure 3.2a) (0.99 and 0.95). For *A. dealbata*, a similar observation was made with respect to the second-order relationship (r^2 = 0.95 and 0.93 respectively, Figures 3.2 b, a). Once again, the relationship was better described by the second- than the first-order regression (r^2 = 0.95 and 0.90 respectively).

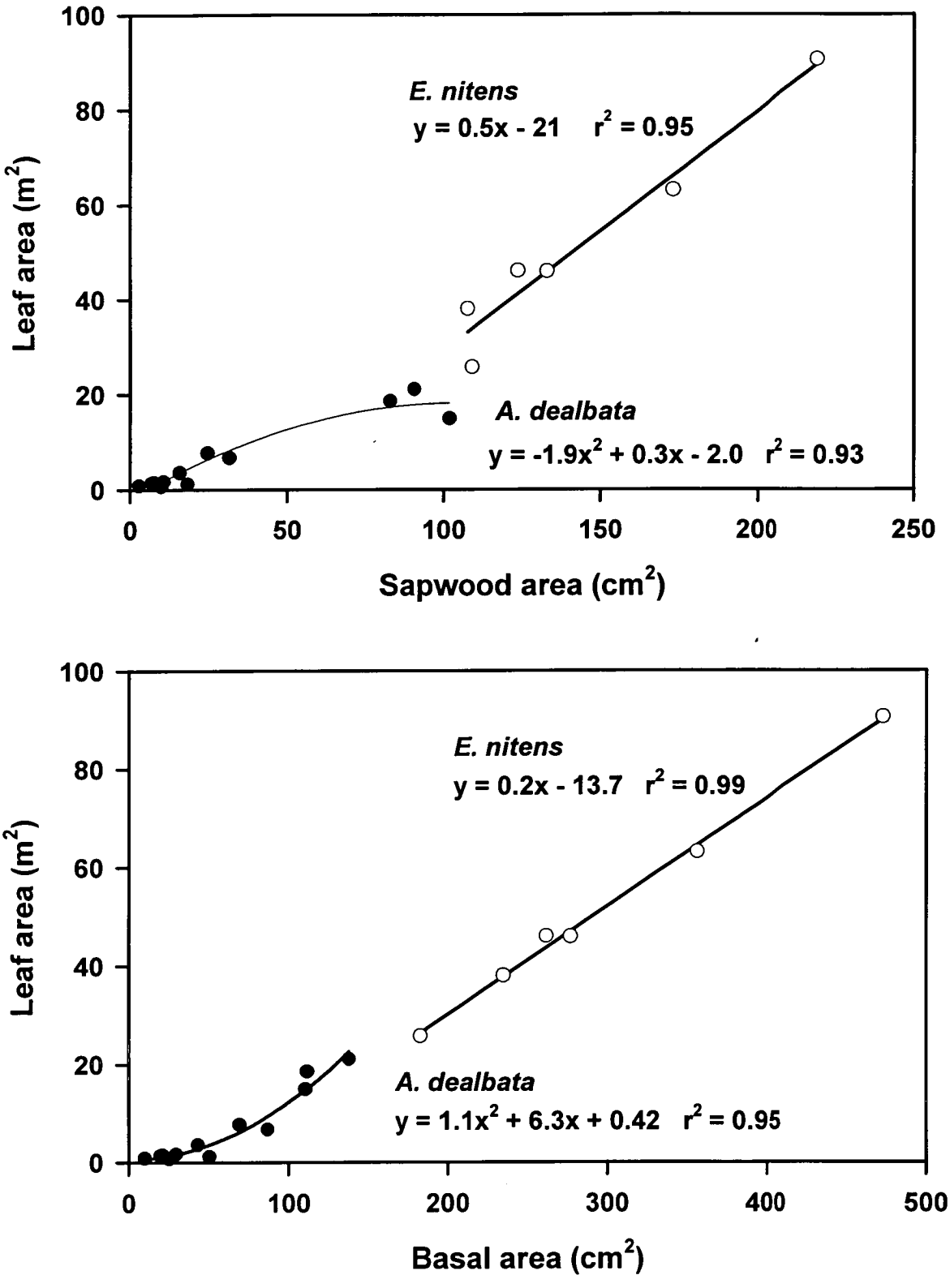


Figure 3.2 The regression relationships between stem variables and tree leaf area for 7-year old trees destructively sampled at Sites 1 and 2 in 1995. (a) The relationship between basal area and tree leaf area for *E. nitens* (Sites 1 and 2 combined) and *A. dealbata* (Site 1); (b) the relationship between sapwood area at breast height and tree leaf area for *E. nitens* (Sites 1 and 2 combined) and *A. dealbata* (Site 1).

1996 data

Branch cross-sectional area was more closely correlated with branch leaf area than either branch length or branch length and csa combined for all treatments (SAS GLM). Accordingly csa was used as the scaling variable (Table 3.2).

Table 3.2 Regression results for relationships between branch cross-sectional area (csa) and leaf area. All data were log transformed and equations are significant to the 0.001 level. The trees were harvested in 1996.

Species	Planting date	Site/Plot	Crown zone	Slope	Intercept	r^2
E. nitens	1988	1	Upper	1.9	1.32	0.79
			Middle	2.38	0.92	0.89
			Lower	2.23	0.9	0.75
	1992	4/U	Upper	2.54	0.52	0.72
			Middle	2.13	1.38	0.85
			Lower	2.19	1.17	0.72
	1992	4/T	Upper	0.88	1.93	0.5
			Middle	1.26	2.32	0.7
			Lower	2.3	1.08	0.78
A. dealbata	1988	1	Upper	1.86	1.25	0.87
			Middle	2.22	0.84	0.75
			Lower	2.48	0.05	0.55
	1992	4/U	Upper	1.49	1.54	0.59
			Middle	2.67	1.18	0.92
			Lower	2.59	0.46	0.89

Highly significant regression relationships were found between leaf area and basal area of *A. dealbata* and *E. nitens* in both 4-year-old (Figure 3.3a) and 8-year-old (Figure 3.3b) trees. Regression relationships were also developed between leaf area and sapwood area at breast height (Figure 3.4), cross-sectional area at the crown base (Figure 3.5) and sapwood

area at the crown base (Figure 3.6). For eucalypts at Site 1 and at Site 4/Plot T, the consideration of these stem variables did not return significantly better relationships than basal area.

Individual regression equations for *A. dealbata* at Site 4/Plot U (4-year old) and at Site 1 (8-year old) did not describe either the relationship between basal area and leaf area nor between sapwood area (at crown base) and leaf area significantly better than a single equation. The same result was returned for a comparison of *E. nitens* in *Acacia*-free (Plot T) and *Acacia*-infested (Plot U) 4-year old plots at Site 4. Separate regression equations were significantly better descriptors of these relationships when species comparisons were made at both ages (i.e. at Site 1 and at Site 4/Plot U). Whilst separate regression equations were necessary to describe the relationships between basal area and leaf area for *E. nitens* at Site 1 (8-year old) and Site 4/Plot U (4-year old), a single equation was adequate for description of the relationship between sapwood area (at crown base) and leaf area for trees of both ages (Table 3.3).

Table 3.3 r^2 values for regression relationships between stem variables and leaf area.

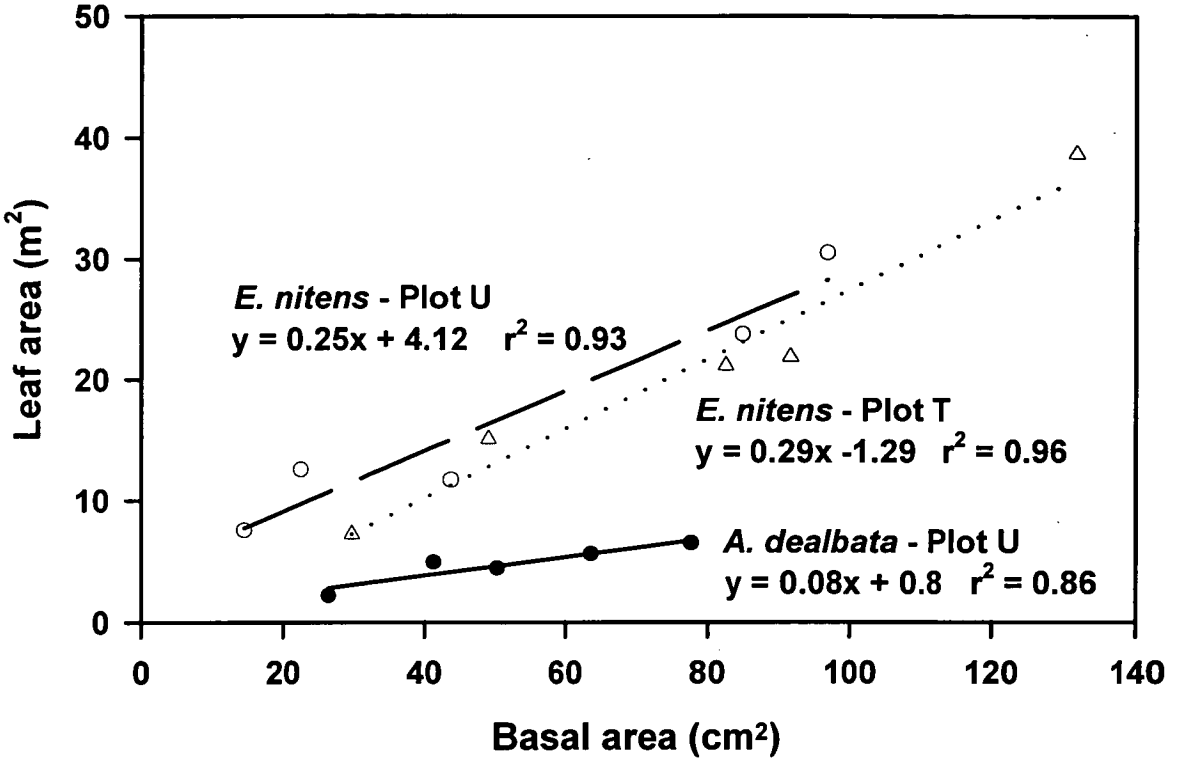
Species	Site/Plot	Planting date	Basal area	Cross-sectional area (crown base)	Sapwood area (breast height)	Sapwood area (crown base)	Average
A. dealbata	4/U	1992	0.86	0.91	0.87	0.96	**0.90**
A. dealbata	1	1988	0.93	0.98	0.9	0.97	**0.95**
E. nitens	4/U	1992	0.93	0.97	0.95	0.94	**0.95**
E. nitens	4/T	1992	0.96	0.9	0.95	0.93	**0.94**
E. nitens	1	1988	0.99	0.96	0.96	0.95	**0.97**
Average			**0.93**	**0.94**	**0.93**	**0.95**	

The ratio of mean leaf area to mean sapwood area (A_l:A_s) was calculated for the five treatments for 1996 data (Table 3.4). *A. dealbata* exhibited significantly lower ($p < 0.05$; t-test) A_l:A_s ratios than *E. nitens* in stands of both ages (1998- and 1992-planted). Differences within species among treatments were not significant.

Table 3.4. Mean leaf area (m^2) to mean sapwood area (cm^2) ratio (A_l:A_s), 1996 data

Species	Site/Plot	A_l:A_s	Standard error (n=5)
A. dealbata	Plot U	0.11	0.02
	Site 1	0.13	0.03
E. nitens	Plot T	0.35	0.05
	Plot U	0.56	0.23
	Site 1	0.29	0.09

Relationships were also examined between basal area and leaf area in individual crown zones. For the middle crown zone, significant relationships were returned for all five treatments. Regressions were non-significant in all but Site 4/Plot U eucalypts for the upper crown zone and significant for Site 1 and Site 4/Plot T eucalypts in the lower crown zone (p at least < 0.05 in all the above cases).



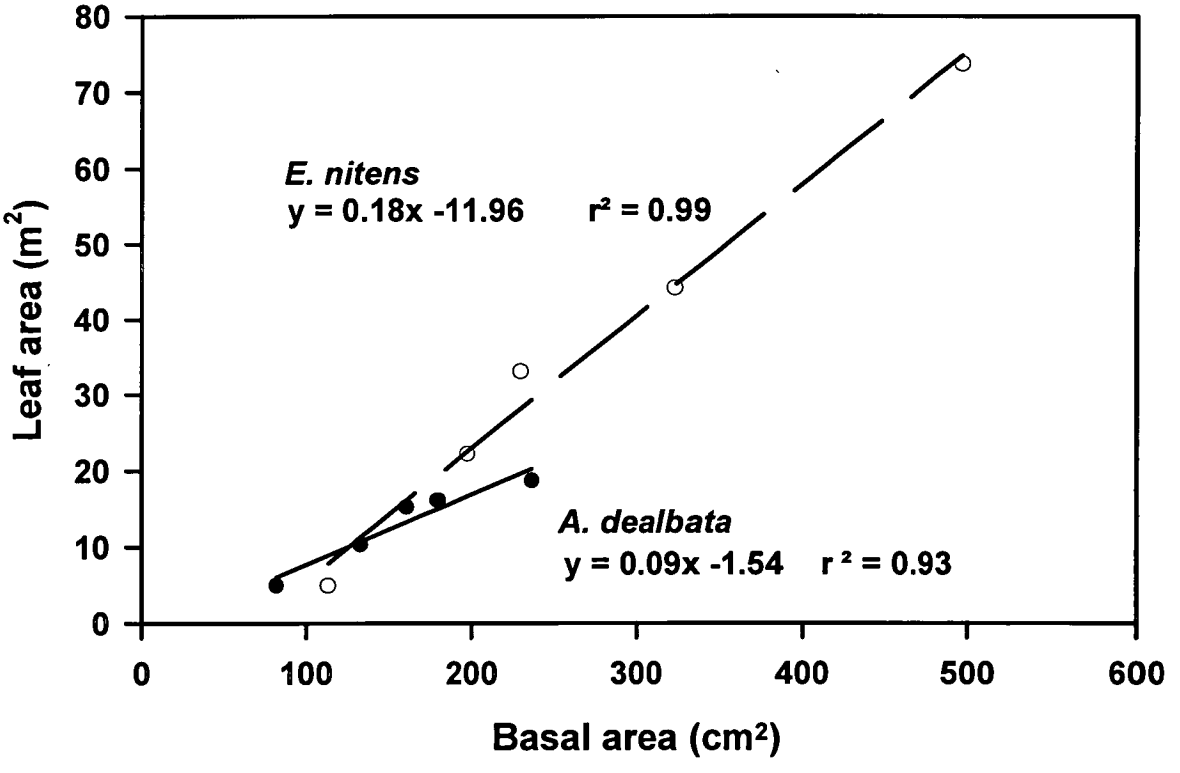
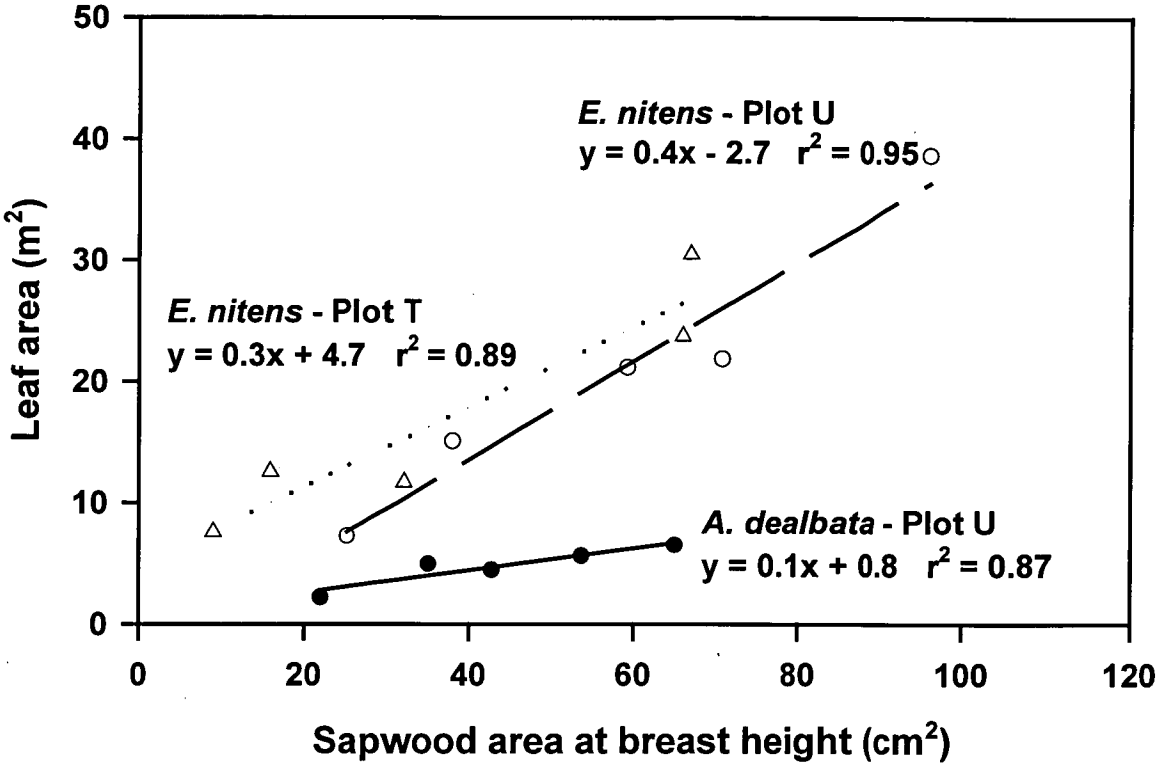


Figure 3.3 The linear regression relationships between basal area and tree leaf area for (a) 4-year old trees at Site 4 and (b) 8-year old trees at Site 1; trees destructively sampled in 1996.



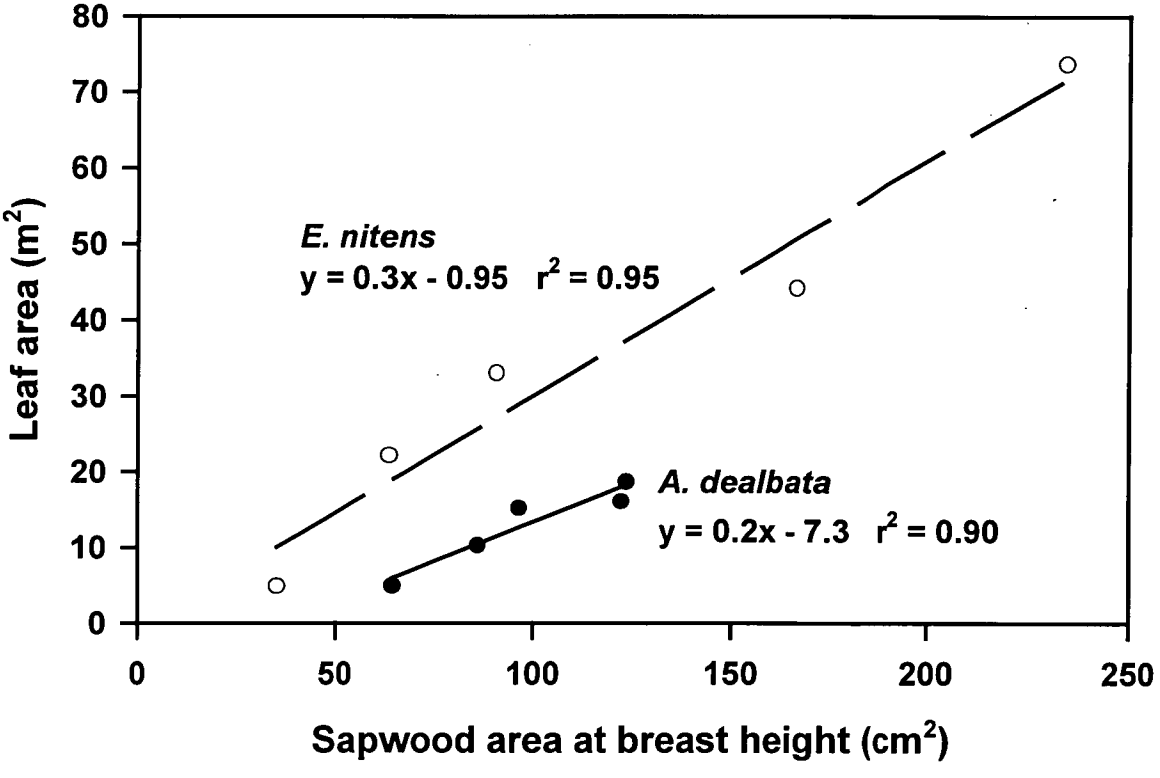
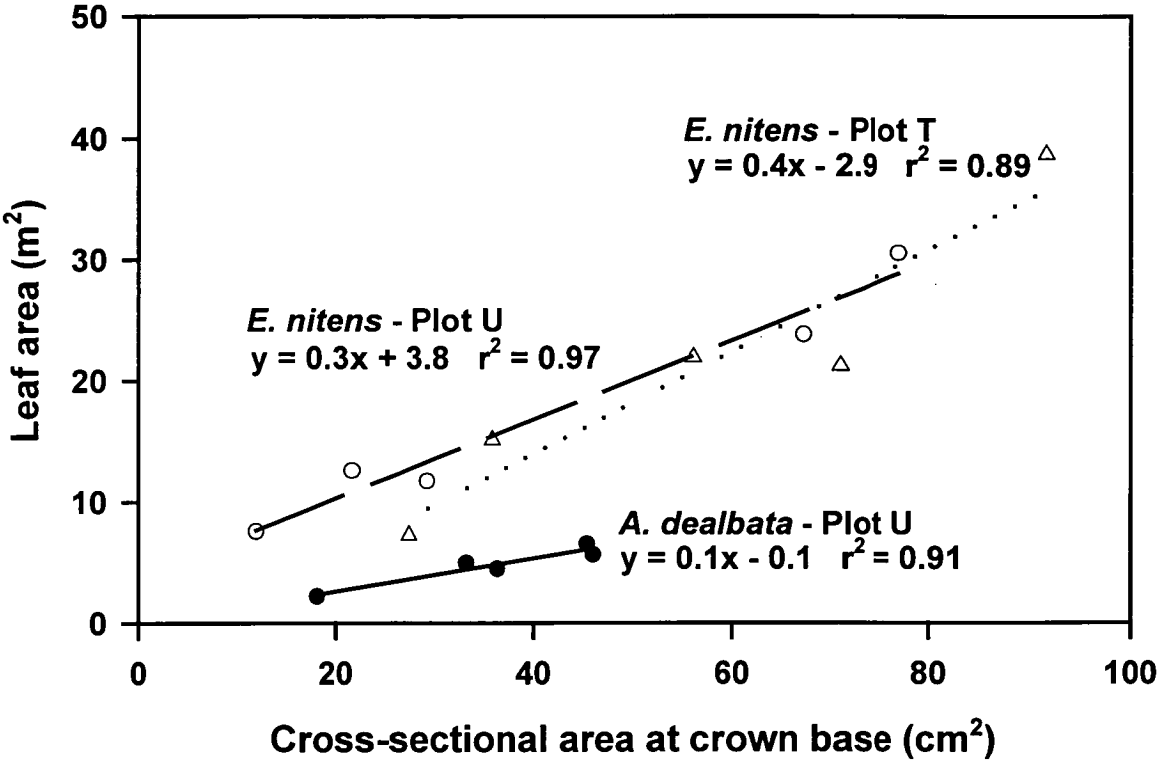


Figure 3.4 The linear regression relationships between sapwood area at breast height and tree leaf area for (a) 4-year old trees at Site 4 and (b) 8-year old trees at Site 1; trees destructively sampled in 1996.



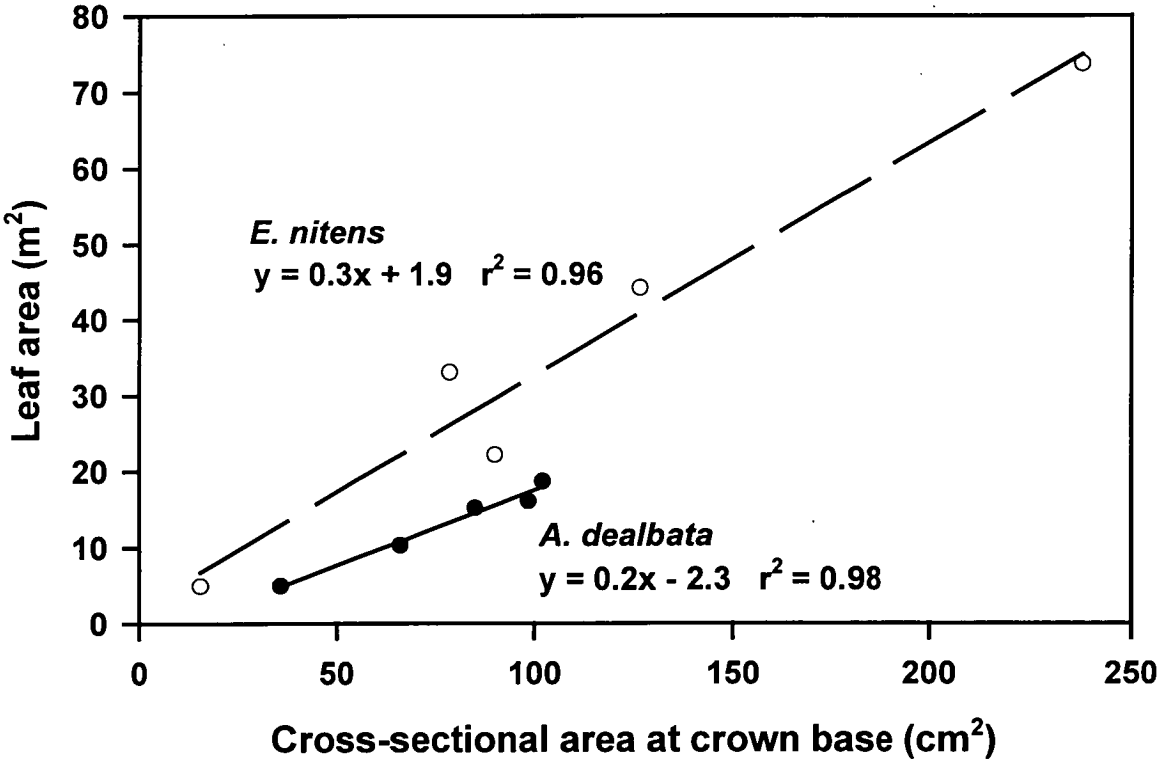


Figure 3.5 The linear regression relationships between cross-sectional area at the crown base and tree leaf area for (a) 4-year old trees at Site 4 and (b) 8-year old trees at Site 1; trees destructively sampled in 1996.

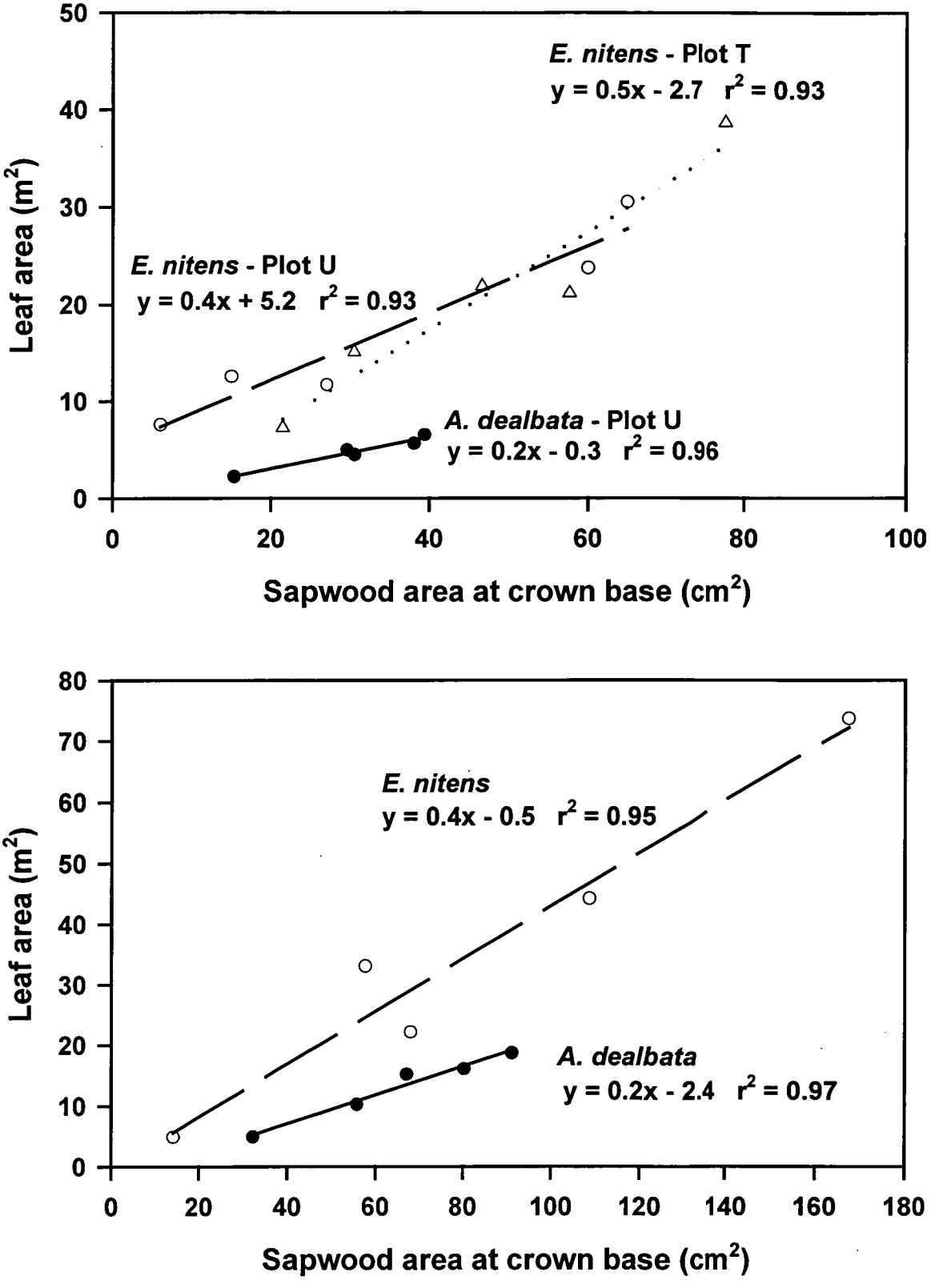


Figure 3.6 The linear regression relationships between sapwood area at the crown base and tree leaf area for (a) 4-year old trees at Site 4 and (b) 8-year old trees at Site 1; trees destructively sampled in 1996.

3.4 Discussion

Specific leaf area of *E. nitens* was consistently and significantly higher than *A. dealbata* though the magnitude of variation was not marked and values for both species fell within the range reported elsewhere for *E. nitens* (Cherry et al. 1998). Importantly, the presence of a dense *A. dealbata* canopy was not reflected in increased values of SLA for *E. nitens* in Plot U (compared to Plot T), even in the lower third of tree crowns. This result indicates a reduced capacity for *E. nitens* to morphologically respond to light at the foliar level (*sensu* Givinish 1987). Therefore, the trend of increasing SLA with crown depth (which was consistent at Site 4 regardless of *Acacia* presence or absence) may be related more to leaf age than to morphological plasticity.

The ratio A_l:A_s (i.e. the slope of the relationship between sapwood area and leaf area) differed markedly between the two species. Whilst published values are unavailable for *A. dealbata*, Beadle and Mummery (1989) and White et al. (1997) both reported similar values for *E. nitens* to those reported in this study. The reduction in A_l:A_s from 0.56 to 0.29 for 4-year old and 8-year old trees respectively for *E. nitens* in *Acacia*-infested plots is consistent with the reduction in this ratio with age reported by Beadle and Mummery (1989). Such a reduction in A_l:A_s has been hypothesised as associated with an increase in allocation of sapwood to storage with distance from the crown base (Hillis 1987). A_l:A_s in Plot T more closely reflected that for the older trees at Site 1 than the Plot U trees of the same age (though this relationship was not statistically significant). White et al. (1997) demonstrated that an increase in A_l:A_s may result from water limitation due to a rationalisation of the sapwood required to meet the hydraulic needs of stomatally limited foliage. Thus, *E. nitens* under intense *A. dealbata* competition in Plot U may have experienced greater water limitation than competition-free eucalypts in Plot T. However, as sapwood measurements used to calculate the ratio were taken at breast height, and as

eucalypts in Plot U exhibited much more crown lift than those in Plot T, the difference may simply be due to the lack of consideration in the ratio of sapwood taper from breast height to crown break.

Tree leaf area was significantly related to all stem variables measured and stem cross-sectional area was found to be a comparable predictor of leaf area to sapwood area (either at breast height or crown base) for both species in all plots. Taken across plots and species, sapwood area at the crown base was the best predictor of leaf area, followed by cross-sectional area at the crown base. The two variables measured at breast height were of equal value. i.e. in the populations sampled, for better prediction of leaf area than that obtained using basal area, measurement of sapwood area at breast height was inferior to csa at the crown base. This is important, as sapwood area is functionally related to leaf area and csa is not. Nevertheless, there are several reasons why sapwood area is not always a better predictor of leaf area than a simple cross-sectional area measurement and, furthermore, why the measurement of sapwood area may not be as useful. When sapwood area is determined from cores, any irregular shape of the heartwood reduces the accuracy of the measurement. For instance, White (1996) and Baldwin (1989) have both reported a minimum of two cores being necessary to account for the ellipsoid shape of *Eucalyptus globulus* and *Pinus taeda* respectively. Furthermore, when sampling of sapwood is required several times during a growing season or in successive growing seasons, sapflow may be severely disrupted and associated experiments confounded (eg for heat pulse experiments). The heartwood boundary in the present study was irregular in most trees sampled, and more so in *Acacia*-infested plots than *Acacia*-free plots, in older than in younger stands and in *A. dealbata* than in *E. nitens*. Even stained discs may not yield unequivocal results. Sapwood may provide a storage role in the stem for carbohydrates (Kramer and Kozlowski 1979) and the differentiation between functional and non-

functional sapwood may be difficult. The functional relationship between sapwood area and leaf area is further confounded by within-stem variation in a range of variables including sapwood permeability (Pothier et al. 1989; Shelburne et al. 1993) and hydraulic conductance (Coyea and Margolis 1994). Such issues further complicate the capacity to establish strong predictive relationships.

Basal area was the superior predictor of leaf area for *E. nitens* in the 1988-planted *Acacia*-infested plot (Site 1) and in the 1992-planted *Acacia*-free plot (Plot T). As noted above, trees in Plot T had deep crowns with little variation in height to crown base. The lack of significant stem taper therefore rendered the basal area measurement as good a predictor of leaf area as csa at the crown base for these trees. However, at Site 1, leaf area was also better predicted by the basal area measure, and a similar explanation is not valid. The difference may be due to the younger eucalypts in Plot U being under more intense competition or in a more transient phase of competition from *A. dealbata* than the older trees at Site 1, thus exhibiting more crown lift and greater variation in stem characteristics generally. Any additional noise in the system is more likely to be accounted for by using a measure at the crown base for building the allometric relationship.

The general utility of the allometric relationships developed in this study reflects the results of a range of recent studies conducted in both hardwood and softwood systems (e.g. Gilmore et al. 1996, Pereira et al. 1997). Strong treatment-specific relationships were developed between leaf area and each stem variable considered. But within each species, a single regression relationship predicting tree leaf area from sapwood area at the crown base was an adequate descriptor of all treatments. Notably, greatest application of a crown base measure has been found not only when transporting relationships between stands of different densities but also in particularly dense stands. This may be because variation in lifting of crowns introduced by high stem density (within populations) or variation in

density itself (among populations) influences the degree of stem taper between breast height and crown height (Maguire and Hann 1990). In the present study, very large differences in stand density were apparent between Plots T and U at Site 4. However, a single regression equation was suitable for describing the *E. nitens* basal area:leaf area relationship in the two stands, i.e. recourse to a sapwood area measure or a measure at crown break was unnecessary. Furthermore, competition was likely to have been heaviest among *A. dealbata* stems (rather than between *A. dealbata* and *E. nitens* or among *E. nitens* – see Chapter 1). Consequently, variations in crown base and stem taper were more pronounced among *A. dealbata* within and between populations. It would therefore be anticipated that sapwood area at crown base would be the most accurate predictor of leaf area for acacias. Whilst this was the case, *A. dealbata* in stands of two ages with very different stem densities were equally well described by a single regression equation as by separate equations.

In order to model leaf area across the range of treatments for each species, the variation in sapwood characteristics between breast height and the crown base required consideration in the regression models. The relationship between sapwood area measured at the crown base and tree leaf area has been found to be independent of site for *E. nitens* (White et al. 1997, Cherry et al. 1998, Medhurst et al. in prep.). Similar site independence of tree allometry has been identified for *Fagus sylvatica* L. (Bartelink 1996) and *Pseutotsuga menziesii* (Mirb.) Franco (Bartelink 1997). Whilst the measure at crown base has been demonstrated as particularly useful for predicting leaf area (eg Maguire and Batista 1996), stem taper can be accounted for by using crown height as a covariate of a basal measurement thus enabling greater application of the method to routine sampling exercises (Medhurst et al. in prep.).

For scaling, both sapwood area and basal area may be the most useful predictors of leaf area and the choice of scaling variable is dependent on the experimental objectives. The measurement of sapwood area (or volume) is particularly useful in studies where productivity modelling is important. Sapwood volume may be used as a correlate of respiration with leaf area a correlate of productivity and thus the relationship between the two may provide an estimate of stand growth efficiency (Ryan 1989, 1990; Ryan and Waring 1992). However, for experiments where an estimate of stand leaf area (or its distribution) is the objective, little advantage is gained by using sapwood area instead of basal area (Dean and Long 1986; Shelburne et al. 1993). Basal area is well recognised as the most easily measured tree dimension and thus has a strong practical role in scaling exercises of this type (Tucker et al. 1993; Shi and Cao 1997).

With regard to the hypotheses tested in this study, sapwood area may be a better predictor of leaf area than stem csa but the differences between the two in this experiment were small. For scaling, the extra sampling required to obtain sapwood values is not warranted and basal area is satisfactory. Should tighter relationships be desired, additional sampling effort should be directed to diameter measurement at the crown base for conversion to cross-sectional area values. When a crown base measure of sapwood area was used to model tree leaf are in this study, neither age nor presence of competition statistically warranted the use of separately derived regression relationships for either species. However interspecific differences in the relationship between stem variables and tree leaf area precluded the use of a general model to satisfactorily describe both species.

Chapter 4. Canopy structure and architecture 2: Crown form, leaf area index and the vertical distribution of leaf area

4.1 Introduction

The relationships established in Chapter 3 enable a consideration of the distribution of leaf area in the mixed stands. Bimodal distributions of plant size such as those identified in Chapter 2 may be attributed in part to the different radiation environments experienced by dominant and subdominant trees and reflect a two tiered canopy structure that results from competition for light (Ford and Newbould 1970; 71).

Whilst both root and shoot competition may be important, canopy structure and competition for light have been the focus of most recent work in competitive systems. This is partly because of inherent difficulties with studying root interactions (Caldwell 1987). However, shoot competition has long been known to cause growth reduction in suppressed species independently of root competition (Donald 1958) and in many systems is considered to be of primary importance (see Section 1.2).

Studies have shown variously that neighbour biomass (Gaudet and Keddy 1988), neighbour architecture (Caldwell 1987) and neighbour light interception ability (Tremmel and Bazzaz 1993) may be the variables most highly correlated with the performance of a target plant. The importance of any of these variables in determining a competitive outcome is the extent to which light is distributed in the canopy, not only in terms of its capture and use by a given plant (the latter will be considered in Chapter 7), but also in the degree to which neighbour plants are deprived. Thus proportional capture of the resource is dependent on the relative placement of plant parts (Tremmel and Bazzaz 1993) and "even an old leaf (or dead one) may play a part in the success of one plant overtopping a neighbour if it deprives the neighbour of light" (Harper 1989). In the present system,

therefore, even if *A. dealbata* were suppressed at canopy closure by *E. nitens*, the moribund stems would be likely to reduce the productivity of the crop species in the short term.

Where light is limiting, the capacity of a plant to alter patterns of resource allocation, or to exhibit morphological plasticity may influence its ultimate success. This is in part because crown construction is a compromise in determining the optimum ratio of foliage biomass to crown surface area (Makela and Albrektson 1992). As the canopy radiation environment changes during stand development and as individual trees move from one dominance class to another, long-term survival of a tree may be dependent on the capacity to alter this relationship between foliage biomass and crown surface area. For example, small crowns have less costs (construction and maintenance) but self-shade and reduce ventilation and therefore reduce the productivity capacity of the tree (Cannell 1989). Therefore, it is advantageous for a tree that is shaded to retain height growth at the cost of foliage and branch growth (Albrektson and Valinger 1985) as trees having tall narrow crowns markedly reduce self-shading (Kuuluvainen 1991). Thus the capacity to alter patterns of above-ground resource allocation not only confers a competitive advantage in a light-limited environment but also indicates a degree of shade tolerance.

In this chapter, the implications of leaf area distribution, crown morphology and canopy architecture are discussed with respect to competition for light between the two species.

The experiments reported test the following three hypotheses:

1. *A. dealbata* makes a greater contribution to total leaf area in young stands than *E. nitens*

2. *A. dealbata* leaf area is concentrated in a light limited environment in older stands

3. *A. dealbata* exhibits morphological and growth characteristics indicative of greater shade tolerance than *E. nitens*.

4.2 Materials and methods

4.2.1 Crown and stem data

Data were collected from the forty three trees sampled for experiments in the previous chapter during winter 1995 and 1996. For the 1995 sampling, additional data on the height to the first live branch (h_c) were collected. Thus, calculation of total crown height could be made in the same manner as for 1996 even though the designation of crown zones differed (see Chapter 3). Crown shape and tree dimensions were described by consideration of the ratio of crown width at the widest point (w_c) to green crown length (l_c) as well as the ratio of l_c to tree height (h_t) and the stem height:diameter ratio (h_t/d). Additional data collected for growth studies (Chapter 2) were used for scaling. The reader is also referred to Figure 7.2 for a pictorial representation of tree dominance classes. In this context canopy position has been used as a relative rather than an absolute term. Sub-dominance and understorey are in relation to the eucalypt canopy rather than a specific height above ground.

4.2.2 Measurement of canopy light penetration

An array of light sensors was used to quantify the extinction of light within the 8-year-old mixed eucalypt/acacia canopy (Site 1) in summer-autumn 1996. Eight sensors were placed vertically at 2 m intervals from the top of the canopy to a depth of 10 m which was below the bases of all tree crowns of both species except for a very small number of moribund understorey acacias. Sensors were placed at the ends of 1.2 m long aluminium struts attached and placed at right angles to a 25 m tall scaffolding tower (on the northern aspect – refer to Chp. 7, pg 109). The struts were approximately vertically aligned and held the sensors in a position between crowns rather than within crowns to as great an extent as the

canopy structure would allow. In this way, the measurements were intended to be indicative of the light environment surrounding outer crown leaves on subdominant and understorey trees. A programmable data logger (Campbell Scientific, Logan, Utah) sensed PPFD (photosynthetic photon flux density) every ten minutes and recorded hourly and daily totals. Records were obtained for a total of 30 days.

4.2.3 Scaling and estimation of LAI

Correlation and regression analyses were used to examine the distribution of leaf area within the canopy by layer. The relationships developed between leaf area and basal area established in the previous chapter were used with basal area data (Chapter 2) to calculate the leaf area of trees within the associated growth plots. Individual tree leaf areas within plots were summed and projected over plot area to estimate leaf area index (LAI) at each site and to apportion LAI between species.

Total height (h_t), green crown length (l_c) and diameter (*d*) data were available for *E. nitens* in the 8-year old *Acacia*-infested stand at Site 1 and *d* data were available for *A. dealbata* in the same stand (data not shown). Regression equations describing the relationships among crown zone, leaf area and basal area (Chapter 3) were used to apportion total crown leaf area to crown zones for eucalypts in a 192 m^2 plot (Plot B, Site 1). Relationships were also derived between *A. dealbata* basal area and both tree height and green crown length. These equations were applied to basal area data for the same plot and the resultant crown dimensions used to estimate vertical distribution of leaf area within crown zones as for the eucalypts. For all trees in the plot, the leaf area estimated within each zone was divided by the length of that zone to return an estimate of leaf area/0.1 m vertical layer (assuming equal distribution of leaf area within each zone). The leaf area estimate for each 0.1 m layer in the mixed canopy (from 7.0 m - 25.0 m) was then summed.

4.3 Results

4.3.1 Crown and stem dimensions

Dimensions of 1995-sampled trees are summarised in Table 4.1. Limited replication and the fact that the samples were stratified reduced the opportunity for meaningful statistical analyses among plots and sites. However, certain trends were evident.

Table 4.1 Crown and stem dimensions of trees destructively sampled in 1995

Date planted	Species	Total Height (m)	Crown width (m)	Height to crown base (m)	Green crown length (m)	Crown width/ crown length	Green crown length/ Total height
1988	*A. dealbata*	9.89	1.7	5.41	4.48	0.38	0.45
	(Site 1)	10.99	1.5	7.13	3.86	0.39	0.35
		11.19	1.73	8.99	2.2	0.79	0.20
		7.92	1.2	5.65	2.27	0.53	0.29
		9.32	1.75	6.33	2.99	0.59	0.32
		7.65	1.41	4.84	2.81	0.50	0.37
		15.3	1.8	10.62	4.68	0.38	0.31
		14.94	2.25	7.99	6.95	0.32	0.47
		14.8	1.9	8.15	6.65	0.29	0.45
		16.22	3.05	9.5	6.72	0.45	0.41
		15.02	3.35	6.5	8.52	0.39	0.57
		17.46	2.62	11	6.46	0.41	0.37
	E. nitens	21.4	3.1	8.82	12.58	0.25	0.59
	(Site 1)	19.2	2.8	8.73	10.47	0.27	0.55
		19.44	2.65	9.7	9.74	0.27	0.50
	E. nitens	17.25	3.35	4.8	12.45	0.27	0.72
	(Site 2)	18.25	2.65	9.35	8.9	0.30	0.49
		18.5	3.9	6.25	12.25	0.32	0.66
1992	*A. dealbata*	7.86	1.45	1.54	6.32	0.23	0.80
	(Plot U)	7.5	1.5	2.4	5.1	0.29	0.68
		8.45	2	1.3	7.15	0.28	0.85
	E. nitens	7.95	2.8	0.29	7.66	0.37	0.96
	(Plot U)	8.85	2.3	1	7.85	0.29	0.89
		7.15	1.45	0.45	6.7	0.22	0.94
	E. nitens	7.53	1.4	2.4	5.13	0.27	0.68
	(Plot T)	6.8	1.55	2.17	4.63	0.33	0.68
		8.38	2.05	2.3	6.08	0.34	0.73

For 1988-planted eucalypts, crowns were proportionally deeper (green crown length/tree height - l_c/h_t) at Site 2 than at Site 1 and maximum width was similar, resulting in a slightly higher width:height ratio (w_c/h_t) where *Acacia* was absent. At Site 1, *E. nitens* had

significantly deeper crowns (l_c/h_t) than codominant *A. dealbata* ($p < 0.05$, t-test) and a significantly lower ratio of w_c/h_t ($p < 0.01$; t-test). In the same stand, understorey *A. dealbata* had much reduced l_c/h_t compared to canopy acacias (dominant and subdominant combined, $p < 0.001$; t-test) and significantly higher ratio w_c/h_t ($p < 0.05$; t-test).

For the 1992-planted trees (Site 4), no significant differences were detected among eucalypts or between eucalypts and acacias in terms of crown width or w_c/h_t. However, *E. nitens* in the *Acacia*-infested plot (Plot U) exhibited significantly shallower crowns (lower ratio of l_c/h_t) than eucalypts in the *Acacia*-free plot – Plot T ($p < 0.05$; t-test).

The stem height:diameter ratio (h_t/d) was significantly higher for *E. nitens* in the presence than in the absence of *Acacia* competition for trees of both ages, but not significantly different between *A. dealbata* and *E. nitens* in plots of either age ($p < 0.05$, t-test; data not shown). At Site 1, for understorey *A. dealbata*, the ratio h_t/d was significantly higher than for canopy *A. dealbata.*

For 1996 data, t-tests did not detect significant differences in green crown length (l_c) between treatments (Table 4.2). However, for 1992-planted trees, l_c was more variable in *E. nitens* from the *Acacia*-infested plot (Plot U) than either associated *A. dealbata* or *E. nitens* in the *Acacia*-free plot (Plot T). Similarly, for 1988-planted trees, l_c of *E. nitens* was more variable than the associated codominant (canopy) *A. dealbata* (Table 4.2). In the 1988 planting (at Site 1), *A. dealbata* had a significantly higher ratio h_t/d ($p < 0.05$, t-test; data not shown) than *E. nitens*. There were no significant differences in h_t/d within or between species for 1992 plantings (Site 4, Plots T and U).

Table 4.2 Crown dimensions of trees destructively sampled in 1996

Date planted	Species	dbh (cm)	Total Height (m)	Crown height (m)	Green crown length (m)	Green crown length/height	Height/ dbh
1988	*A. dealbata*	7.25	20.2	10.59	10.34	0.71	1.36
		9.00	18.46	9.32	9.14	0.63	1.16
		8.00	19.14	10.77	8.37	0.66	1.16
		5.80	15.87	9.87	6.00	0.55	1.70
		9.95	18.95	9.85	9.10	0.65	1.30
	E. nitens	17.35	24.35	10.7	13.7	0.51	1.77
		14.30	15.95	11.13	4.82	0.50	1.78
		13.00	18.3	8.8	9.5	0.44	2.09
		10.20	18	9.71	8.29	0.38	2.35
		15.10	21.4	11.3	10.1	0.48	1.69
1992	*A. dealbata*	10.25	8.82	2.6	6.22	0.78	1.04
		6.15	8.84	3.3	5.54	0.73	1.24
		12.95	7.87	2.7	5.17	0.75	1.02
		7.90	8.17	3.65	4.52	0.75	1.20
		10.80	9.91	3.5	6.41	0.68	1.12
	E. nitens (Plot U)	5.35	6.89	1.79	5.1	0.74	1.31
		10.40	11.02	2.94	8.08	0.73	1.19
		11.10	11.21	2.8	8.41	0.75	1.13
		7.45	8.58	3.5	5.08	0.59	1.41
		4.30	7.82	2.47	5.35	0.68	2.01
	E. nitens (Plot T)	25.15	9.85	2.16	7.69	0.56	1.40
		12.00	7.3	1.94	5.36	0.30	3.58
		15.85	11.02	2.81	8.21	0.52	1.71
		17.10	8.13	2.04	6.09	0.46	1.80
		20.30	9.49	3.04	6.45	0.47	1.69

4.3.2 Vertical distribution of leaf area within crowns

Acacias in the 1988 planting at Site 1 had a more even vertical distribution of leaf area than acacias in the 1992 planting at Site 4 (Figure 4.1), with a significantly greater proportion of their crowns in the lower zone ($p < 0.05$), less crown in the middle zone ($p < 0.01$) and more crown in the upper zone ($p < 0.01$). The distribution of leaf area within the 1992-planted eucalypt crowns did not differ significantly between *Acacia*-infested and *Acacia*-free plots. However, there was significantly more leaf area in the upper crown zone

of eucalypts at Site 1 than at Site 4 (Plots T and U; $p < 0.01$). When eucalypts at Site 1 were compared only with those in the *Acacia*-infested plot at Site 4 (Plot U), an associated significant ($p = 0.01$) reduction in middle crown leaf area was apparent. Leaf area was more evenly distributed among lower and middle crown zones for *E. nitens* than for *A. dealbata* at Site 4, leaf area in the latter being concentrated in the middle zone. There were no significant differences in leaf area distribution between *A. dealbata* and *E. nitens* at Site 1.

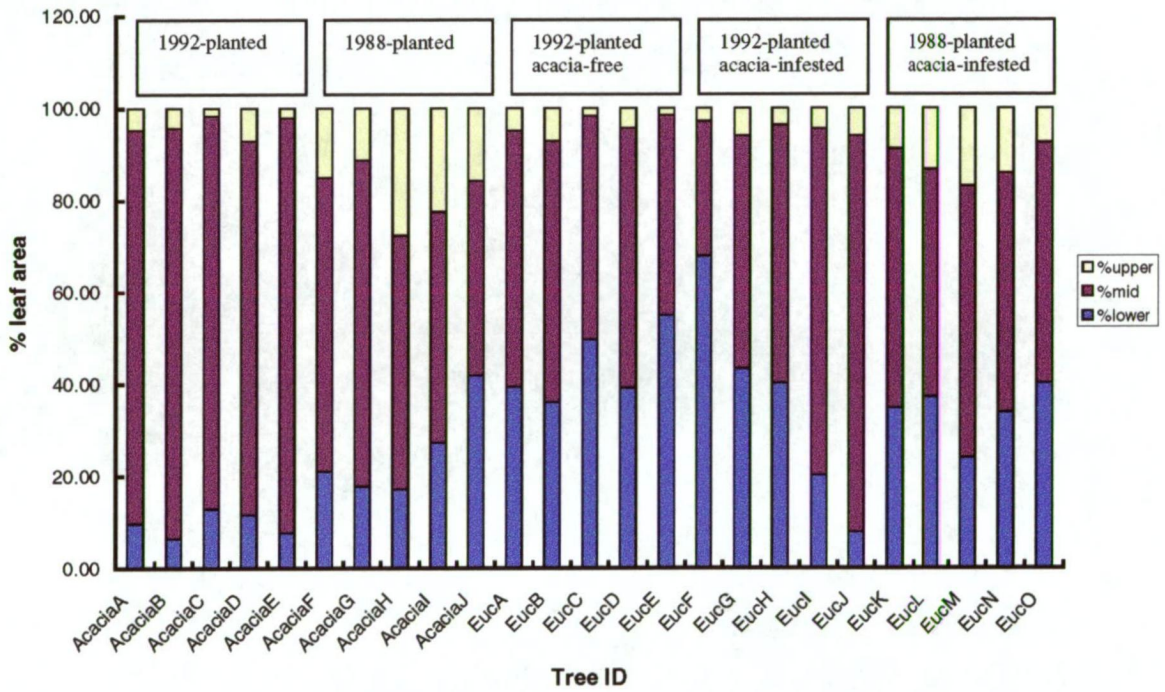


Figure 4.1. The proportional distribution of leaf area among crown zones for destructively sampled trees in 1996. Eucalypts A-E - Plot T, Site 4; Acacias A-E, eucalypts F-J - Plot U Site 4; Acacias F-J, eucalypts K-O, Site 1.

4.3.3 Vertical distribution of leaf area within the mixed canopy

Vertical distribution of leaf area for both species was unimodal and positively skewed (skewness 0.35 and 0.2 for *A. dealbata* and *E. nitens* respectively). Over 90% of *E. nitens* leaf area was located between 13.5 m and 21 m above ground with nearly 20% of that leaf area concentrated between 16 m and 17 m above the ground. For *A. dealbata*, 90% of leaf area fell between 8 m and 16 m above the ground, the highest concentration within any 1 m zone similarly being almost 20% of the total for that species, but occurring between 13 m and 14 m height above ground (Figure 4.2). The zone of overlap between the two species (between 12 m and 19 m above ground – 40% of the canopy depth) held 70% of the *A. dealbata* plot leaf area and 78% of the *E. nitens* plot leaf area, the remaining portions being respectively below and above the mixed species part of the canopy.

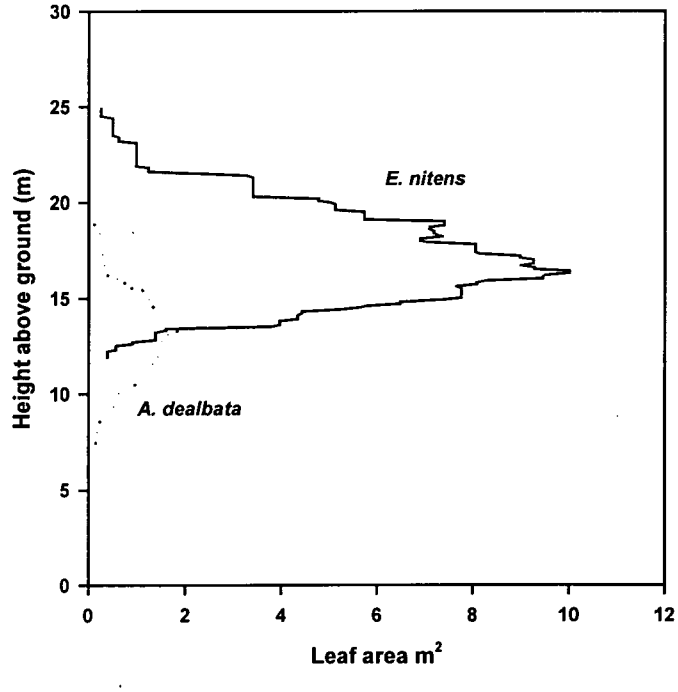


Figure 4.2. Vertical distribution of leaf area in a mixed *Acacia/Eucalyptus* plot at Site 1 (age 8 years).

4.3.4 Vertical distribution of PPFD

Patterns of light distribution were similar for all transects sampled, daily variation being associated with weather variables and hourly variation associated with weather variables and sun angle (data not shown). Typically, the amount of transmitted light was reduced markedly between 4 m and 6 m below the top of the canopy (16 m to 20 m above the ground) and again between 6 m and 8 m (14 - 16 m above the ground) (e.g . Figure 4.3a & 4.3b).

Beer's Law was applied to the PPFD data:

$$k = -\{\ln Q_i/Q_o\}/LAI$$

where Q_o and Q_i are incident PPFD at the top and base of the canopy respectively. LAI was calculated for the stand from allometric data (below) and an extinction coefficent (k) of 0.65 was returned based on an integrated approach to Q_i/Q_o. PPFD was not measured at the top of the *Acacia* canopy (19 m) but at 20 m and 18 m above ground. On cloudless days, at midday, the proportion of total PPFD incident at 20 m above ground varied between 65% and 80% (mean 74%) of maximum. However, at 18 m above ground, incident PPFD had fallen to less than 15% (range 8% - 14%, mean 11%) of that incident on the top of the *E. nitens* canopy. At 08:00 hours, PPFD incident at 20 m was generally 10% lower than at midday (63% - 69%, mean 66%) and 24% - 29% of total PPFD was incident at the 18 m stratum (mean 26%). At 16:00 hours, PPFD at 20 m and 18 m was as little as 30% and 6% respectively of that incident at the top of the canopy. The large variation between morning and afternoon values reflected horizontal heterogeneity in the canopy and changes in sun position.

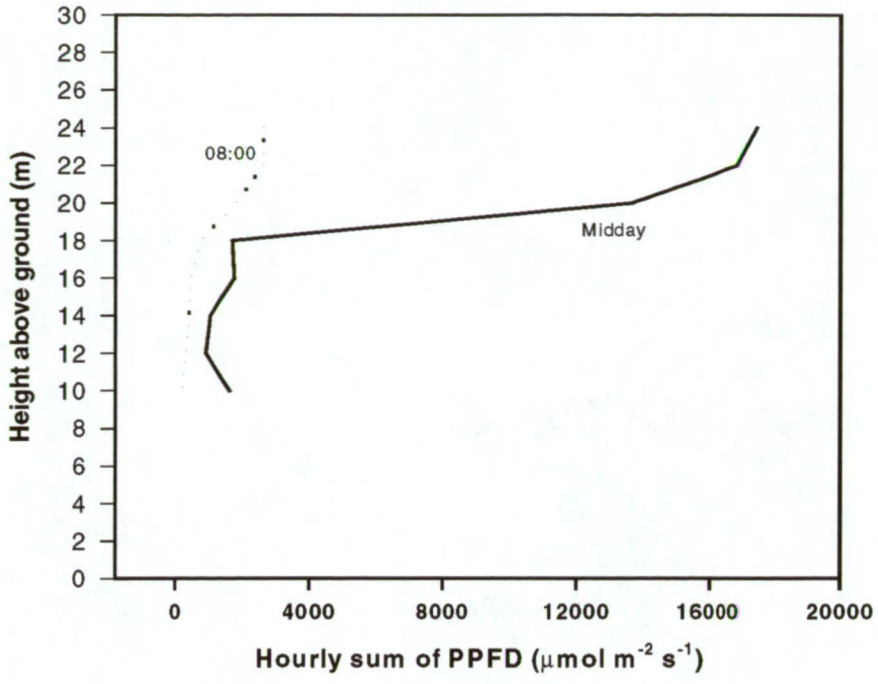


Figure 4.3a. Variation in hourly incident PPFD (summed from point measurements at five minute intervals and averaged over an hour) on 27/3/96 from the top to the base of the canopy in early morning and at midday at Site 1 in an 8-year-old mixed *Acacia/Eucalyptus* plot.

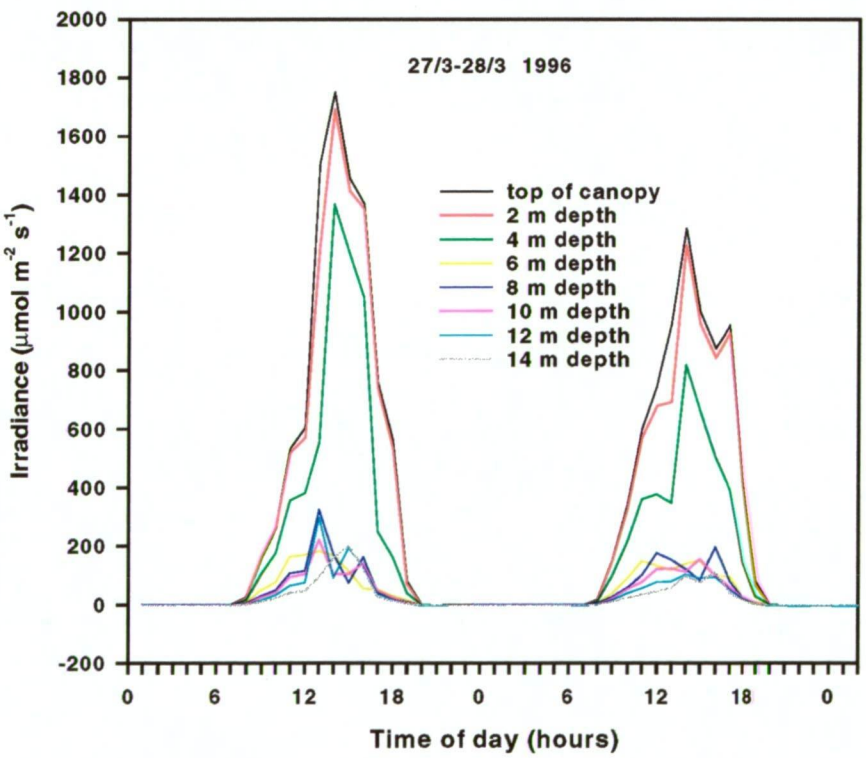


Figure 4.3b. Diurnal course of PPFD (from point samples at five minute intervals) in a mixed *Acacia/Eucalyptus* plot at Site 1 (age 8 years). Values are averages for one hour periods (30 min either side of the annotated time).

4.3.5 Leaf area index (LAI)

For 1995, in nine 7-year-old plots with high *Acacia* density (at Site 1), average *E. nitens* LAI was 2.7. At the same time, the average LAI for the five *Acacia*-free plots at Site 2 was 4.3. For 1996, in six 8-year-old plots, for which basal area data were available (at Site 1), *A. dealbata* contributed an average 20% of a stand LAI of 3.4 (Table 4.3). LAI of *E. nitens* at Site 1 plots remained stable over the two measurement years, with differences between years not significant (t-test). An estimation of *A. dealbata* LAI was not available for 1995 due to the absence of basal area data for that year. However, application of allometric relationships developed in Chapter 3 to interpolated basal area data from 1994 and 1996 (Chapter 2) yielded estimates of LAI for 1995 (data not shown) not significantly different to those obtained for 1996 ($p > 0.05$; t-test).

Table 4.3 Relative contribution of *A. dealbata* and *E. nitens* to estimated values of stand LAI.
(see Chapter 2 for full plot descriptions)

1995

Site 1	*E. nitens*	Site 2	*E. nitens*
A	2.3	J	4
B	3.0	K	4.6
C	3.3	L	4.4
D	2.6	M	3.9
E	2.4	N	4.5
F	3.4		
G	2.0		
H	2.0		
I	2.9		
average	2.7		4.3

1996

Site 1	*E. nitens*	*A. dealbata*	*Plot Total*
B	2.9	0.9	**3.7**
C	3.3	0.7	**4.0**
F	3.2	0.3	**3.5**
G	2.0	0.3	**2.3**
H	2.0	1.0	**3.0**
I	2.8	0.8	**3.6**
average	**2.7**	**0.7**	**3.4**

Site 4	*E. nitens*	*A. dealbata*	*Plot Total*
U	1.3	1.5	2.9
T	2.5		2.5

In a single 4-year-old plot for which 1996 data were available (at Site 4, Plot U), *A. dealbata* contributed just over 50% of a total LAI of 2.9 (Table 4.3). In the corresponding *Acacia*-free plot (Site 4, Plot T) the *E. nitens* LAI was 2.5, 86% of canopy LAI in the adjacent Plot U but nearly twice the LAI of the eucalypt component of that plot.

4.4 Discussion

A. dealbata was an important contributor to LAI in both 4-year-old and 8-year-old stands, though the relative contribution was markedly reduced with age. In the 8-year-old stand, *A. dealbata* leaf area was concentrated in the lower middle of the canopy. In this position, most of the available light had already been intercepted by the bulk of the eucalypt canopy and the uppermost portion of the *A. dealbata* canopy. Whilst *A. dealbata* was a co-dominant tree in the 4-year-old stand, its canopy position was sub-dominant in the 8-year-old stand, with important implications for its continuing ability to actively compete with the eucalypts.

Increases in tree height:diameter ratio may be associated with decreasing light availability (Wang et al. 1994). This is due to the preferential allocation of photosynthate to height growth in order to maintain a dominant canopy position. Whilst it is observed in both shade tolerant and shade intolerant species, it is less apparent in the former. Shade tolerant species more often direct resources to lateral growth in order to harvest more of the radiation available in the light-limited sub-canopy environment (Chen 1997). They also generally show greater plasticity in resource allocation, favouring leaf development over below-ground or structural investment (Tanouchi 1996). Higher ratios of h_t/d evident at Site 1 than at Site 2 and at Site 4 in Plot U than in Plot T thus provide an indication of greater light limitation for *E. nitens* in the presence than in the absence of *A. dealbata*.

Furthermore, the shift from similar h_t/d ratios for *A. dealbata* and *E. nitens* in 1995 to higher ratios for the former species in 1996 (at Site 1) suggests that light limitation is increasing with time for acacias. Understorey *A. dealbata* at Site 1 exhibited proportionally wider crowns (higher ratio of w_c/h_t) than canopy acacias, conforming to the above model that emphasises the capturing of available light in the more limiting light environment. Notably, these understorey *A. dealbata* also exhibited higher h_t/d ratios than their upper canopy counterparts. These data suggest that the change in resource allocation from stems to foliage occurs after trees are fully suppressed. Supporting this hypothesis was the morphology (refer to ratios in Tables 4.1; 4.2) of subdominant *A. dealbata* which possessed morphologies approximating dominant rather than understorey trees. Importantly, understorey *A. dealbata* were generally moribund and growth was normally restricted to epicormic shoots in small gap environments. Thus the likely success of *A. dealbata* as a persistent understorey tree is questionable in spite of the apparent shift in resource allocation.

The rate of crown lifting in a stand is a function of stem density (Maguire and Hann 1990). Due to a more favourable balance between respiratory costs (associated with the sapwood volume) and potential photosynthetic gains (foliage area), deeper crowns facilitate higher growth efficiencies (Maguire and Batista 1996). Thus, in the present study, higher ratios of l_c/h_t indicate not only reduced competition between trees but also indicate potentially higher productivity. *E. nitens* exhibited higher L_c/H_t ratios in plots where *A. dealbata* was absent (Site 2 > Site 1; Plot T > Plot U). This provides further evidence for light limitation of *E. nitens* by *A. dealbata* in *Acacia*-infested plots. Furthermore, *E. nitens* exhibited higher l_c/h_t than *A. dealbata* in plots where both species occurred. Whilst greater growth efficiency for *E. nitens* is suggested by these data, the reduced stem volumes for *A. dealbata* (indicated by relative h_t/d ratios above) may have reduced respiratory costs

sufficiently to balance this interspecific difference. A reduced hydraulic capacity brought about by a relatively reduced sapwood volume could also lower the productivity of *A. dealbata* (Whitehead and Jarvis 1981).

Crown shape differences between species have been observed to signify successional status (Fujimoto 1993). For both species considered in this study, crowns were essentially spheroidal. This was indicated by the concentration of leaf in the middle crown zone which has been widely reported for a range of species (eg Jarvis and Leverenz 1983). Such a result infers that the two species occupied similar niches, but even for trees of similar height and crown shape, it is the relative distribution of leaf area among crown zones that determines tree canopy position and thus competitive advantage (Yokazawa et al. 1996). Differences between species (and between eucalypts at *Acacia*-free and *Acacia*-infested sites) in the relative distribution of leaf area among crown zones was largely absent in this study. This result both emphasises the similarity in growth habit of the two species and indicates (in light of other data presented) that within-crown leaf area distribution is not a useful indicator of dominance in this system. Furthermore, the similarity in vertical leaf distribution for *E. nitens* in both Plot U and Plot T indicates a lack of response in crown shape to *A. dealbata* presence at age 4 years. Both species did, however, possess more leaf area in the upper crown zone in 8-year old (Site 1) than 4-year old (Site 4) plots. This was probably due to the region of rapid shoot growth constituting a smaller proportion of the total green crown length in the older trees rather than any change in resource allocation *per se*.

In the *Acacia*-infested plots, the two species occupied the same canopy stratum in the 4-year old stand (Site 4, Plot U), whilst in the 8-year old stand (Site 1) the *Acacia* canopy was clearly subdominant to the eucalypt canopy. This reflects a change in the relative success of the two species in the years immediately following canopy closure. The vertical

arrangement of foliage in the older stand (Figure 4.2) is indicative of a very efficient mixed canopy (in terms of radiation interception), with pendulous leaves dominant in the upper layer (*E. nitens*) and horizontal leaves dominant in the lower layer (*A. dealbata*) (Li et al. 1997). This efficiency was reflected in the extinction coefficient calculated from the light distribution data (0.65) which was higher than the value normally used in equations predicting leaf area for eucalypt canopies (0.5, eg Gazarini et al. 1990; White 1996). Pinkard et al. (1998) reported that 95% of incident PPFD was intercepted by an *E. nitens* canopy with an LAI of 4 ($k = 0.53$). In the present study, 90% of incident radiation was intercepted by a canopy with an LAI of just 3.4, further indication of efficient light interception by a mixed canopy.

LAI of the 8-year-old stand (Site 1) was similar to that estimated for an 8-year-old coppiced stand of *E. globulus* (Pereira et al. 1987) and for a mixed *Eucalyptus* spp/*Acacia longifolia* regeneration forest (Wong and Dunin 1987). The authors of the latter study estimated that *A. longifolia* contributed 14% to a total stand LAI of 3.3 in a 12-year-old forest, very similar to the present study. In that study, as in the present one, the acacia canopy was concentrated below the bulk of the eucalypt canopy. For 4-year-old stands (Site 4), estimates of LAI were less than those reported elsewhere for eucalypts of similar age. Beadle and Mummery (1989) reported a maximum LAI of 6 for *E. nitens* at 4 years of age and White (1996) reported an LAI of approximately 4 for 3-year-old *E. nitens* growing on a water-limited site. However, in both cases, stocking was considerably higher than in the present study, resulting in more advanced canopy development at that age.

The first two hypotheses stated in Section 4.1 were supported by the results discussed above. However, there was little indication that *A. dealbata* was a more shade tolerant species than *E. nitens*. *A. dealbata* contributed half the total leaf area in the 4-year-old

mixed stand but only 20% of the leaf area in the 8-year-old stand. In the 8-year-old stand, *A. dealbata* leaf area was concentrated near the base of the *E. nitens* canopy. The *A. dealbata* canopy had clearly been suppressed by age 8 years. The crown morphology and growth habit of neither species was indicative of adaptation to an understorey environment and those acacias which had been suppressed were unsuccessful in the very low radiation found in the subcanopy environment. However, as the remaining *A. dealbata* canopy becomes suppressed, the radiation environment in the understorey may become more favourable due to the simplification of the overstorey canopy structure and consequent reduction in overstorey light interception. Thus those acacias which are last to be suppressed may persist as an understorey as the stand ages.

Chapter 5. Canopy structure and architecture 3: Accurate area determination of complex leaves using digital image analysis

5.1 Introduction

As stated in section 3.1, accurate determination of crown or canopy leaf area is essential for the scaling up of individual leaf measurements in many hydrological, productivity and physiological studies (Grier and Running 1977; Waring et al. 1981; Wang et al. 1995). Much attention has been given to the problem of adequately describing the three-dimensional distribution of foliar elements within canopies (eg Smith et al. 1993) and the associated difficulties and approaches have already been discussed in this thesis. However, the accuracy of measurement of individual leaves has received less consideration in the literature (Kvet and Marshall 1971; Larsen and Kershaw 1990) and is particularly relevant in this study where acacia leaves with a high level complexity were measured.

Traditionally, planimetry has been the preferred technique for the measurement of one-sided leaf area and a range of commercial devices, such as the Delta-T leaf area meter (Delta-T Devices Ltd, Cambridge, England) and the Licor LI-3000 area meter (Licor Inc, Lincoln, Nebraska), is available for this purpose. Such instruments use photographic- or videographic-type lenses to measure the area of light occluded by a leaf based on a surface grid of varying resolution. Assuming frequent calibration of the instrument during measurement, radial distortion and resolution of the lens are potential sources of error with this method. The former is minimised by placing samples close to the centre of the reading frame. The latter is a function of the relationship between instrument resolution and the size of elements to be distinguished (Biscoe and Jaggard 1985). This error is more likely to be significant when dealing with complex or fine leaves rather than broadleaves.

For measurements of fine and needle-leaved species, simple lens-based planimetry may be inadequate, particularly due to parallax errors, and a range of alternative methods has been proposed including computer scanning and image analysis (Kershaw and Larsen 1992). Recently, several dedicated image analysis systems have been developed for area measurement of leaves and roots, employing both camera and scanner systems for image capture (eg Delta-T DIAS and Delta-T SCAN respectively). Such commercial systems have overcome the problems of resolution stated above but may be expensive and can be time consuming to operate when dealing with small foliar elements (Kershaw and Larsen 1992).

In the present study, it became apparent during the 1995 destructive sampling (Chapters 3 and 4) that a technique with finer resolution than was being used to measure leaf area of *E. nitens* was required to obtain accurate estimates for acacia leaves. Consequently, high resolution image analysis was employed in the corresponding 1996 experiment. However, the results obtained were still not entirely satisfactory, as the acacia leaves often presented overlapping pinnae. Consequently, it was deemed necessary to investigate the accuracy of the methods used for leaf area measurement in this study.

For the experiments described in this chapter, two hypotheses were tested:

1 low resolution planimetry is an unsuitable method for the area measurement of *A. dealbata* leaves and

2 inaccuracies of measurement can be overcome by the use of a high resolution image analysis method.

Additionally, the image analysis technique that was developed is described.

5.2 Materials and methods

Leaves of *E. nitens*, pinnae of *Dicksonia antarctica* Labill. and leaves of *A. dealbata* were used for analysis, offering surfaces of low, intermediate and high complexity, respectively.

5.2.1 Experiment 1 - Comparison of methods

A Delta-T leaf area meter was used to estimate area by planimetry (A_p) for a set of custom-built black aluminium plates of different shapes. This instrument has a resolution of 1/300 of the scanned width (about 20 cm in this experiment) which equates to approximately 35 dots per inch (dpi) and uses a high contrast light occlusion technique. Before experimentation the instrument was calibrated using three rectangular metal standards (100 cm^2, 50 cm^2, 10 cm^2) supplied by the manufacturer. Each aluminium plate was placed in the centre of the reading frame and the area measured three times (one measurement series), with each measurement on a different orientation of the plate. Each plate was then measured once at each of the cardinal radii (north, south, east, west) at the extremity of the reading frame. Calibration (in the centre of the reading frame with the supplied standards) was repeated between each measurement series.

The areas of the plates were then remeasured (A_i) using a computer image analysis protocol modified from Hodson et al. (1995). Plates were placed on an Epson®GT-6500 scanner and the images were captured as 16 colour grey scale TIFF files on an IBM-pc computer (80486DX2-66) using the software Epson Scan (V. 1.30). The resolution was constant at 300 dpi and a plain white background was used to ensure colour distinction of the plate edges. An image analysis package (IDRISI V. 4.1) was used to determine the area (cm^2) of the plate in each scan. Captured TIFF images required conversion to IDRISI format using the TIFIDRIS module. The RECLASS module was used to assign the value 0 to all colours except the white background and shadows (which were assigned 15) and the AREA module was used to measure the plate area (ie the area covered by pixels with a

value of 0). The measured area was automatically saved to a text file at the conclusion of the process. A batch file incorporating the three IDRISI modules was used to process the set of scanned images.

5.2.2 Experiment 2 - Optimum scanning resolution

A green broadleaf-shaped paper replica was scanned for image analysis at 22 default resolutions (from 45 dpi to 600 dpi) and a green paper rectangle (42.25 cm^2) was scanned at 9 resolutions over the same range as above. Three replicates each of an *A. dealbata* leaf and a *D. antarctica* pinna were scanned at five resolutions corresponding to those suitable for routine measurement (50, 75, 100, 144, 180 dpi). Images were analysed using the same protocol as in Experiment 1 to return the area of each scanned object.

5.2.3 Experiment 3 - Leaf complexity and crown position

Leaves were sampled from four trees in a mixed *E. nitens/A. dealbata* canopy (at Site 1); one eucalypt, the dominant of the four and three acacias which represented co-dominant, subdominant and understorey canopy classes. Tree crowns were divided vertically into thirds for sampling. Twelve replicate leaves were collected from each of the upper, middle and lower thirds of each of the four tree crowns. All leaves were weighed fresh (W_f), measured individually by image analysis (at 75 dpi with the above methods) and subsequently measured by planimetry. The process was completed within 36 hours of collection. All leaves were oven dried to constant weight at 80°C (W_{80}) prior to determination of specific leaf area (SLA).

Twelve pinnae of *D. antarctica* were excised from a single mature frond. Each was measured in the centre of the planimeter, in three different orientations. The twelve pinnae were then separated into four groups of three. Each group was measured three times in the centre of the planimeter, the pinnae being arbitrarily moved in relation to each other between replicate scans. All pinnae were subsequently measured in the same manner by

image analysis.

5.2.4 Experiment 4 - Dissection of *A. dealbata*

The effect of folding and closing of acacia leaves on measured area (with respect to total area) was assessed on leaves from a subdominant tree (scanning resolution 75 dpi). Three replicates of two representative leaves were sampled from each acacia crown position (18 leaves, 9 samples) and scanned individually (Figure 5.1a). For each pair of representative leaves, the primary pinnae were detached from the primary rachi, separated across the scanner bed so that none overlapped, and rescanned (Figure 5.1b). Two primary pinnae sampled from each leaf in the pair (four pinnae per replicate) were then scanned (Figure 5.1c), prior to detachment and separation of the secondary pinnae and scanning for a fourth time (Figure 5.1d).

For controls, square pieces of card (of known dimensions and area) were measured with the leaf area meter and by image analysis. Three 25 cm^2 squares of card (5 cm x 5 cm) were first measured by the leaf area meter. Each was bisected and remeasured. The process was repeated a further seven times for each replication, yielding 256 elements of an average size of approximately 0.1 cm^2. A subsample of 15 elements was then measured and two further bisections undertaken, yielding the equivalent of 1024 elements of 0.024 cm^2 average area (based on 25 cm^2 original). Three 100 cm^2 squares (10 cm x 10 cm) were measured using the image analysis method (above). Each was subsequently bisected and remeasured 8 times (that is 512 elements, average size of approximately 0.19 cm^2). A subsample of 15 elements was bisected and remeasured a further 4 times yielding elements of the same final size as for the leaf area meter controls (0.024 cm^2, see above). Each image was scanned at 6 resolutions and all images were adjusted digitally to account for shadow. Where sub-sampling was undertaken (for both the leaf area meter and image analysis), results were expressed as a proportion of the area of original card.

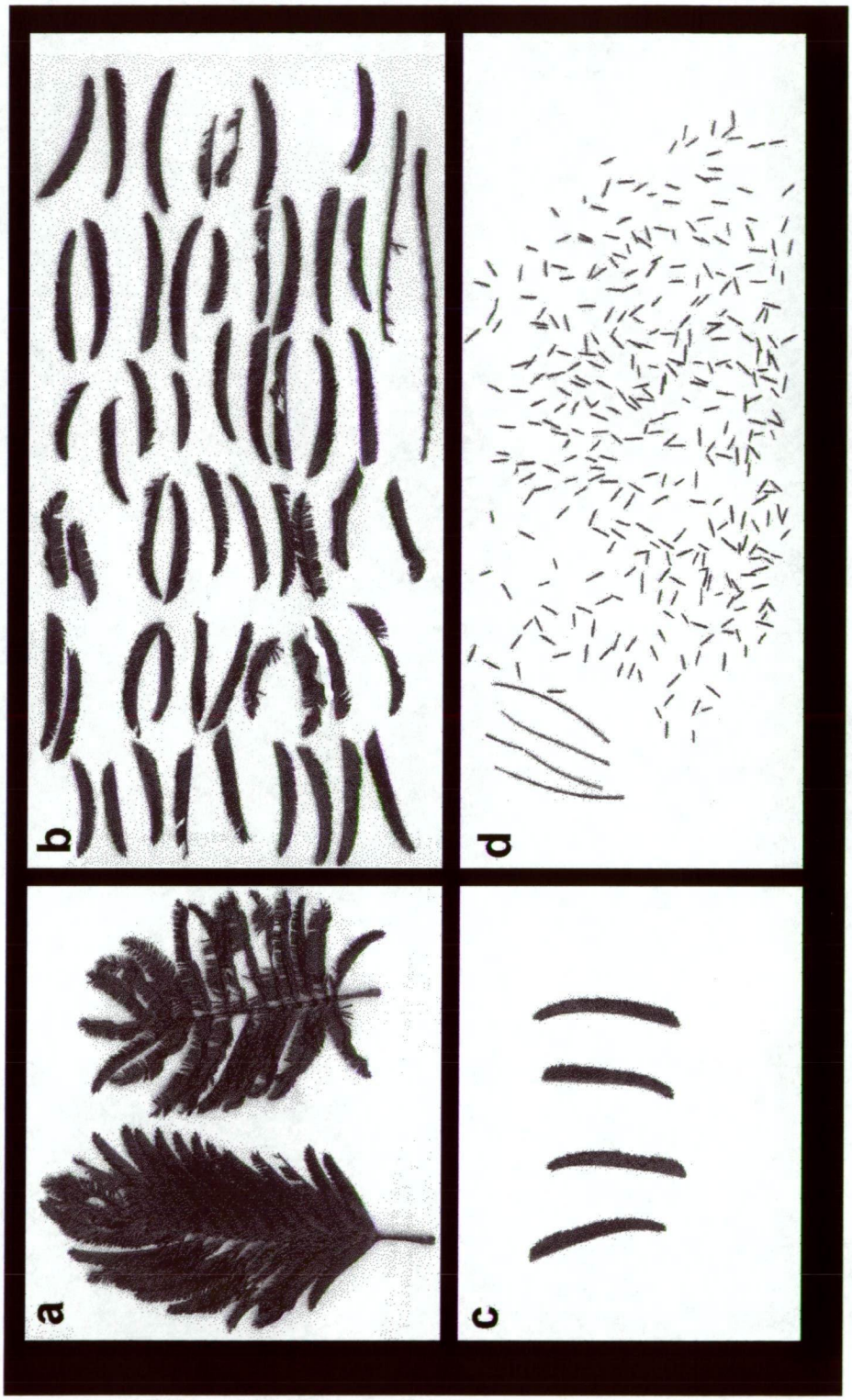


Figure 5.1. The progressive dissection of the *Acacia dealbata* leaf, from intact leaf (a) to component primary pinnae (b); primary pinnae subsample (c) and dissection to component secondary pinnae and rachi (d).

5.2.5 Analysis

Results were analysed using simple descriptive techniques (Experiment 2), t-tests (Experiments 1, 3 and 4) and ANOVA (Experiments 3 and 4). t-tests were all two-tailed; both single factor and replicated two factor ANOVAs were used.

5.3 Results

5.3.1 Comparison of methods

A_p was marginally higher (<1%) at the frame edges than at the centre of the reading frame of the Delta-T planimeter ($p<0.05$). The magnitude of this variation was small compared to the measured differences in area between planimeter and image analysis where the mean ratio A_p/A_i was 0.97 ($p<0.05$, SD = 0.01).

5.3.2 Optimum scanning resolution

Area of the broadleaf replica increased in magnitude from 45 dpi (the lowest resolution) to 400 dpi (with a small decrease from 90 dpi to 120 dpi) before declining to a minimum at the highest scanning resolution (600 dpi) (Figure 5.2a). The paper rectangle returned values closest to the known area (determined geometrically to 0.004 cm^2) when scanned at the lowest resolutions (50 and 75 dpi) and again at very high resolution (Figure 5.2a). The *A. dealbata* series showed decreasing area from 50 dpi to 75 dpi before increasing again to 180 dpi . *D. antarctica* values followed a similar pattern but reached minima at 100 dpi (Figure 5.2b).

The degree of variation in A_i at different resolutions varied among the surface types measured (from 1% - 5% of the scanned area). These differences were associated with the perimeter/area ratio and the size of the scanned elements, the magnitude of the variation being inversely affected by image area. A comparison of A_i with true area was calculated geometrically for the paper rectangle but an independent area measure for leaves was not

possible (but see results for Experiment 4 below). However, the optimum scanning resolution suggested by the standard shape data was 75 dpi. Thus, this resolution was used for subsequent experiments with leaves.

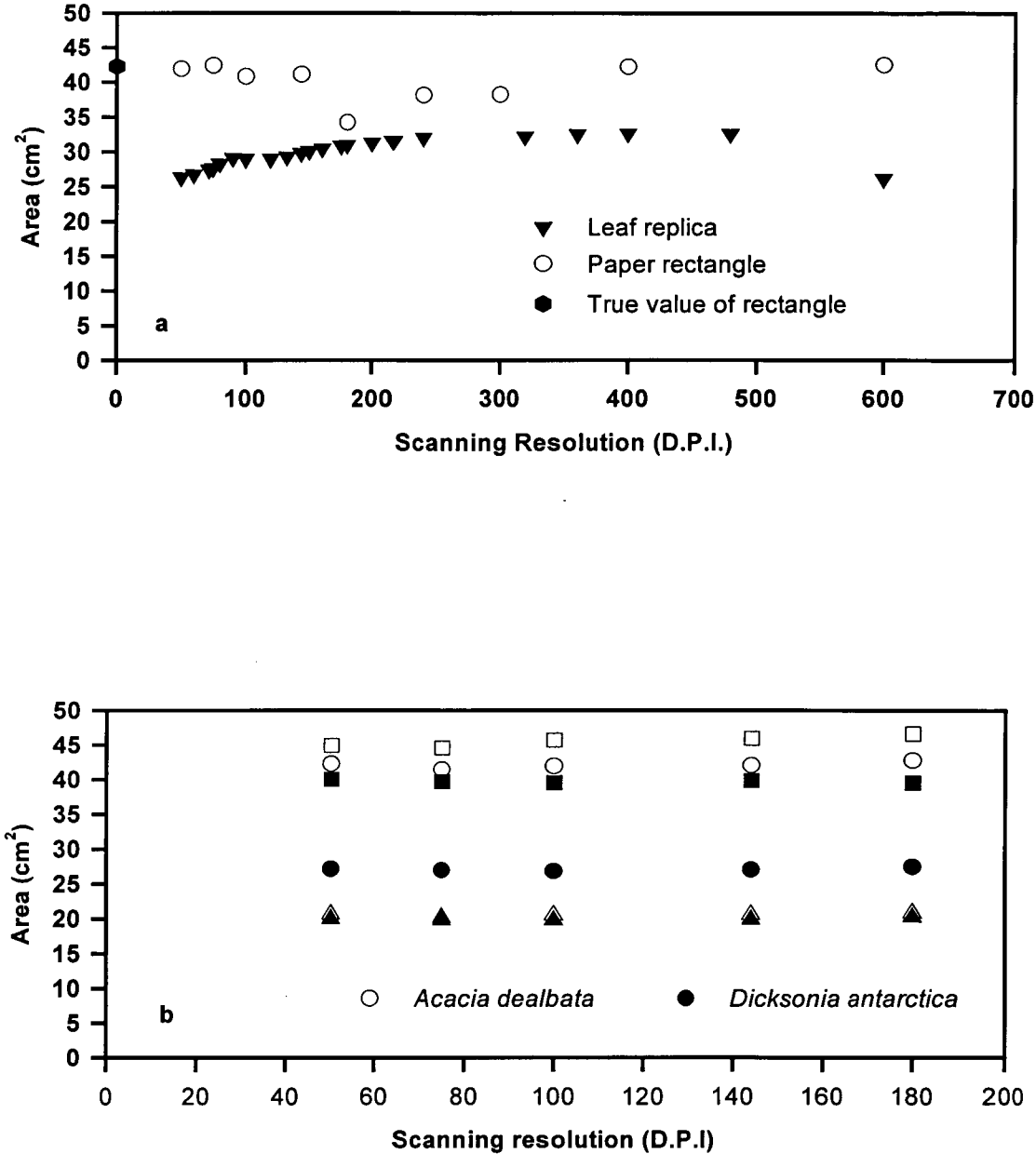


Figure 5.2. (a) The variation in measured area with changes in scanner resolution of (a) a paper broadleaf replica and a paper rectangle of known area and (b) three replicates each of a *Dicksonia antarctica* pinna (open symbols) and an *Acacia dealbata* leaf (closed symbols).

5.3.3 Leaf complexity and crown position

Data for each crown position for the four trees are summarised in Table 5.1. A_p was significantly different to A_i for each of the twelve data sets ($p<0.001$ in all cases). A_p was consistently 97% of A_i for the eucalypt with no significant difference ($p>0.05$) among crown positions. For acacias, A_p varied between 8% and 65% of A_i for individual leaves and the ratio (A_p/A_i) was significantly different among acacia crown positions and canopy classes ($p<0.001$). In each of the three acacia crowns sampled, SLA (calculated using A_i) decreased from the upper crown to the lower crown (Table 5.1). The coefficient of variation did not differ significantly between A_p and A_i among eucalypt crown positions ($p>0.05$). However, significant differences in the coefficient of variation were observed among acacias and crown positions within acacias between A_p and A_i ($p<0.001$). The coefficient of variation of SLA (using A_i) was less than 20% in eight of the nine acacia crown thirds sampled.

The mean value of A_p/A_i for *D. antarctica* was 0.93 (standard error 0.05) for both the twelve individual pinnae and the four pinna groups. There was no significant difference in A_p/A_i between the pinna groups and the sums of the corresponding individual pinna measurements.

5.3.4 Dissection of *A. dealbata*

Dissection of *A. dealbata* leaves to primary pinnae resulted in increases of A_i between 26% and 83% (ratio primary pinnae/intact leaf) with significant differences among crown positions ($p<0.01$) (Table 5.2). Hence, the overlapping of primary pinnae is a large source of error in estimation of true area. Further reduction of primary pinnae to composite secondary pinnae (ratio secondary pinnae/primary pinnae subsample) resulted in

Table 5.1 Variation in leaf area between planimetry (A_p) and image analysis (A_i) methods by species, canopy class and crown position, and calculated values of specific leaf area (SLA) based on A_i. (Values are means. Refer to text for *n* and *p* values.)

Tree ID	Crown third	W_{80} (g)	A_p (cm^2)	A_i (cm^2)	A_p/A_i	SLA (A_i)
E. nitens	Top	1.67	66.61	69.05	0.97	42.19
	Middle	1.92	77.07	80.60	0.96	42.47
	Lower	1.91	83.89	86.95	0.97	45.72
A. dealbata co-dominant	Top	1.52	27.64	50.41	0.55	33.41
	Middle	0.74	24.68	73.88	0.35	108.51
	Lower	0.58	18.17	70.57	0.25	122.33
A. dealbata sub-domin.	Top	0.60	22.03	55.61	0.39	94.26
	Middle	0.59	28.68	75.96	0.37	129.37
	Lower	0.48	14.52	67.07	0.22	141.02
A. dealbata understorey	Top	0.71	22.82	68.21	0.33	98.37
	Middle	0.55	23.96	62.67	0.37	117.81
	Lower	0.50	14.63	69.03	0.21	143.23
D. antarctica	-	-	22.80	23.90	0.93	-

Table 5.2 The effect on measured area of progressively dissecting *A. dealbata* leaves to component primary and secondary pinnae. Leaves were sampled from three crown positions on a sub-dominant tree.

Crown Position		Area (cm^2)					
		Intact leaf	Primary pinnae	Primary pinnae subsample	Secondary pinnae	Primary pinnae/ leaf	Secondary pinnae primary pinnae
Upper crown	Rep1	33.56	56.72	3.24	3.52	1.69	1.09
	Rep2	31.00	54.08	4.70	5.06	1.74	1.08
	Rep3	33.75	53.21	3.99	4.40	1.58	1.10
	Mean					1.67	1.09
	Coef. of Var. (%)					0.007	0.000
Mid crown	Rep1	35.90	52.50	4.73	5.16	1.46	1.09
	Rep2	27.61	34.71	3.36	3.64	1.26	1.08
	Rep3	31.69	44.78	6.03	6.18	1.41	1.02
	Mean					1.38	1.07
	Coef. of Var. (%)					0.011	0.001
Lower crown	Rep1	35.51	58.69	5.38	7.61	1.65	1.41
	Rep2	29.46	51.99	4.88	7.38	1.76	1.51
	Rep3	38.97	71.38	4.90	6.64	1.83	1.36
	Mean					1.75	1.43
	Coef. of Var. (%)					0.008	0.006

significant increases in A_i of less than 10% for upper and middle crown but 43% for the lower crown ($p<0.01$) (Table 5.2).

Measured area of the controls increased with decreasing element size for the leaf area meter down to 0.1 cm^2 element size (Table 5.3a). The measured area subsequently decreased markedly with decreasing element size. For image analysis, a similar trend was evident (Table 5.3b). However, the coefficients of variation were markedly smaller for image analysis compared with the leaf area meter. No significant improvement in the coefficient of variation was achieved by using a scanner resolution of greater than 75 dpi (Table 5.3b).

5.4 Discussion

Significant increases in measured leaf area were obtained by using image analysis compared to planimetry. Greater leaf complexity resulted in larger errors using planimetry or low resolution image analysis. Inadequate instrument resolution was a particularly important source of error when estimating leaf area of *A. dealbata* and was exacerbated by the presence of overlapping pinnae.

Although image analysis can avoid potential sources of error in planimetry, it is not straightforward. For each set of similar images scanned, subjective decisions must be made as to which pixels are to be classified as true image, shadow and background. Increasing complexity of image (particularly with surface depth) leads to increasing difficulty in classification of the shadow/image boundary (Hodson et al. 1995). In addition, increasing resolution does not indefinitely improve the accuracy of the measurement. Beyond an optimum resolution, overestimates and underestimates of true surface area may be observed depending on a number of surface properties. In the present study, the subjectivity of these decisions (pixel classification and optimum resolution) was partly

Table 5.3a Control bisection of paper square to elements Leaf area meter

Bisection number	Number of elements	Mean size of element (cm^2)	Area (cm^2)			
			Rep 1	Rep 2	Rep 3	average
0	1	25.0	25.0	25.0	25.0	25.0
1	2	12.5	25.1	25.0	25.0	25.0
2	4	6.25	25.0	25.1	25.1	25.1
3	8	3.125	25.2	25.1	25.1	25.1
4	16	1.563	25.4	25.3	25.2	25.3
5	32	0.78	25.6	25.5	25.4	25.5
6	64	0.39	26.0	25.6	25.7	25.8
7	128	0.19	26.2	25.6	25.7	25.8
8	256	0.1	26.0	25.8	25.8	25.9
9	512	0.05[A]	12. 5	20. 0	17. 5	16.7
10	1024	0.024[A]	2. 5	7. 5	7. 5	5.8
Co-efficient of variation %			**34.3**	**23.5**	**24.6**	**27.3**

Table 5.3b Control bisection of paper square to elements Image analysis

Bisection number	Number of elements	Mean size of element (cm^2)	Area (cm^2)				
			50 dpi	75 dpi	100 dpi	150 dpi	200 dpi
0	1	100.0	101. 5	101. 5	102. 5	101. 8	101. 5
1	2	50.0	101. 6	101. 6	102. 5	102. 9	103. 1
2	4	25.0	101. 7	101. 8	101. 9	101. 9	101. 4
3	8	12.5	101. 6	101. 2	101. 8	101. 9	101. 9
4	16	6.25	101. 8	101. 5	101. 6	101. 7	101. 7
5	32	3.125	100. 6	101. 1	101. 4	101. 5	101. 6
6	64	1.563	100. 3	100. 9	101. 4	101. 7	101. 6
7	128	0.78	99. 7	100. 5	101. 5	101. 8	101. 7
8	256	0.39	97. 8	99. 6	100. 6	101. 4	101. 3
9	512	0.19	96. 1	98. 8	100. 6	101. 6	101. 5
10	1024	0.1	99. 1	101. 0	102. 8	104. 1	103. 7
11	2048	0.05[A]	96. 7	96. 7	106. 7	107. 0	106. 6
12	4096	0.024[A]	91. 8	97. 8	100. 2	102. 4	102. 0
Co-efficient of variation %			**3.0**	**1.6**	**1.6**	**1.5**	**1.4**

[A] Subsample calculated back to the area of the original square

overcome by consideration of a synthetic surface of known area and of the same colour as the leaves later measured (paper rectangle).

A resolution of 75 dpi was adequate for measurement of leaves of low (broadleaves) and intermediate (fern pinnae) complexity. It was not possible to geometrically determine the area of a reference surface of similar morphology to an acacia leaf and this precluded estimation of an optimum sampling resolution for the most complex surface. In a similar study of conifer needles, Kershaw and Larsen (1992) successfully used a scanning resolution of 100 dpi. However, 75 dpi was used in the present study due to the small variation in measured area over the acacia resolution series and the increased cost in processing time and computing resources associated with higher resolutions. Furthermore, results from Experiment 4 indicated that coefficients of variation were not reduced by increasing scanning resolution beyond this value for elements of the size considered in this study.

Variation in measured area across a planimeter reading frame has been well established and is routinely accounted for in experimental work of this nature (Wolf 1983). However, the magnitude of this variation in the present study (< 1%) was small compared to other errors identified. Resolution was of increasing importance with increasing surface complexity. Hence, mean values of A_p (at 35 dpi) were 97%, 93% and less than 40% of A_i (at 75 dpi) for eucalypt leaves, fern pinnae and acacia leaves respectively.

In addition to potential errors associated with resolution, measurement of acacia leaves is further complicated by their habit of closing around the rachi in response to diurnal rhythms, moisture conditions and mechanical disturbance (Daubenmire and Charter 1942; Robbertse 1972). For these reasons, accurate measurement is logistically very difficult with planimetry (Vertessy et al. 1995). The leaf area of intact acacia leaves was underestimated by almost half due to overlapping and folding of primary pinnae and

significant differences in this underestimation were identified among crown positions. Between tree variation was not considered here but is likely to be important (Kvet and Marshall 1971). If present, it may preclude the establishment of relationships sufficiently robust to apply one correction factor across a sample of trees. Hence, acacia leaves must be reduced to their component pinnae for area analysis. Further division to secondary pinnae increased measured area, particularly in the lower canopy foliage, but it is difficult to attribute these increases in A_i to greater accuracy. The secondary pinnae are elements at the limit of the scanning resolution. Thus an underestimate of A_i is inherently probable (based on control data in Experiment 4) though opposite to the result obtained. Inadequate identification of shadows from the secondary pinnae during image analysis probably contributed to the larger area measured. The equivocal nature of these results and the costs in time and resources associated with reduction to component secondary pinnae prior to measurement suggest that it is not warranted.

Differences in results for crown positions in *A. dealbata* emphasise morphological variation in that species in response to light environment (see Chapter 4). The importance of considering this source of variation when sampling tree crowns has been identified for conifers (Niinimets and Kull 1995; Sprugel et al. 1996) as well as for broadleaves (Pinkard and Beadle, in press). However, the within-crown variation in SLA was small (less than 20% in all but one of nine acacia crowns) compared to variations in SLA resulting from changes in resolution during measurement of leaf area (50% - 1200%) and leaf to pinnae dissection (average 60%). Therefore, in a scaling exercise, emphasis must be placed on obtaining an accurate value of area for a given leaf rather than on the absolute number of leaves included in a canopy sub-sample. The latter has been the traditional approach due to the inherent within-crown variability of SLA (Kvet and Marshall 1971). Where a commercial image analysis system is not available for this purpose, the method described

above may provide a simple and inexpensive solution. The decreasing cost and increasing resolution of digital cameras will soon permit the replacement of the flat-bed scanner in such a method, considerably reducing labour and processing time and thus permitting the use of even higher resolutions with potentially greater accuracy.

The implications of these findings for conclusions made in Chapters 3 and 4 are considerable. Leaf area of *A. dealbata* was concentrated in the middle of the crown. Thus underestimation of tree leaf area will be at the lower end of the scale implied by Table 5.2. It is likely that the contribution *A. dealbata* made to canopy LAI was 50% greater than estimated. In the 8-year-old mixed stand, in which the data presented here were collected, this would raise the contribution of *A. dealbata* to stand LAI from 20% to 30% (Table 4.3).

In terms of the relationships among stem variables and leaf area determined in Chapter 3, a 50% increase in the reported value of *A. dealbata* leaf area would change the slope of the regression equations markedly, but not sufficiently to return higher leaf area:sapwood area ratios for *A. dealbata* than for *E. nitens*.

Implications of the correction factor obtained above have been considered here rather than applied to the original data analysis in Chapter 3 for two reasons. Firstly, the extent of between-tree variation of the correction coefficient was not considered in these experiments and may be sufficiently large to bias corrected results. Accordingly, it was more appropriate to report the measured results (Chapter 3) and identify potential errors (Chapter 5) than to manufacture new results. Secondly, the presentation of data in the original form permits comparison with other studies where low resolution planimetry of the whole leaf was used to measure leaf area (eg Vertessy et al. 1995).

With respect to the hypotheses stated in the introduction (Section 5.1), low resolution planimetry is not a suitable method for determining the area of fine complex leaves such as

those of *A. dealbata*. The data indicate that a scanning resolution of at least 75 dpi is necessary for resolution of elements of the necessary size. However, higher resolution does not overcome the largest errors in the measurement of *A. dealbata* leaves which are associated with the overlapping of primary pinnae, particularly in upper canopy foliage. Reduction of leaves to their component primary pinnae prior to measurement is essential for accurate measurement of their leaf area.

Chapter 6. Whole tree transpiration and water use partitioning

6.1 Introduction

In the preceding 3 chapters, competition for light, which was indicated by results in Chapter 2, was considered. Water was also indicated in Chapter 2 as a potential secondary limiting resource and as such required investigation.

Quantification of stand water use is important for forest management in the context of water yield (Vertessy et al. 1995), species selection (White et al. 1996) and silvicultural management (Whitehead and Kelliher 1991). Consequently, a satisfactory approach is needed to measure and predict the transpiration component of water use at the stand scale where problems of terrain, floristic and structural heterogeneity preclude the use of physical and leaf-level parameterisation models and where scale prevents the use of modern remote sensing approaches at the resolution required. The measurement of whole tree water use by the heat pulse method potentially provides accurate physiological estimates of transpiration by individual plants under such conditions (Hatton and Vertessy 1990), all of which were present at the study site.

As the heat pulse technique has developed (Marshall 1958; Swanson and Whitfield 1981; Swanson 1983), the accuracy and speed of point measurements of sapflow have improved and other sources of error in converting these measurements to whole-tree estimates have become more consequential (Daoqun et al. 1996). The most important component of these errors involves the variation in sapflow velocity with sapwood depth (e.g., Cohen et al. 1985). The first attempt to account for the variation was the fitting of a least squares polynomial to point estimates integrated from several depths (Cohen et al. 1981; Edwards and Warwick 1984; Green and Clothier 1988). However, it is not always possible to

identify such a sap velocity profile with depth (Dunn and Connor 1993). An alternative approach is a weighted average method taking into account the correlation of flow rate with seasonal wood production. This method has been applied in young trees (Hatton et al. 1990; Hatton et al. 1992; Dye 1996). Most recently, Daoqun et al. (1996) described a method for developing correction coefficients using small numbers of sensors to account for radial variation in sapflow. Thus accurate measurements of sapflux may be obtained from routine point measurements.

Nevertheless biometric problems in scaling transpiration from tree to stand are still evident. A variety of approaches has been used, including the use of crown classes (Ladefoged 1963), tree size (Cermak and Kucera 1987) and a combination of stand inventory characteristics such as stem diameter, basal area and sapwood area/leaf area ratios (Hatton et al. 1995). Analyses of the errors associated with such scaling approaches have been investigated by several authors (e.g., Hatton and Vertessy 1990; Hatton et al. 1995). Scaling problems involve identification of elements in the forest that are likely to behave differently due to variation in either physical or physiological controls and finding a satisfactory relationship between sapflux and an easily measured inventory parameter. Both types of problem are increased by the structural complexity of a stand (Hatton et al. 1995) and the rate at which the stand is changing (Teskey and Sherriff 1996).

Although application of whole-tree sapflux measurements is being routinely applied to plantation monocultures (e.g., Dye 1996; Loustau et al. 1996; Teskey and Sheriff 1996), application of this technique to the study of floristically complex forests is more difficult (but see Becker 1996). In the present study, the above techniques were used to estimate the relative contributions to stand water use of *E. nitens* and *A. dealbata* at the sites described in earlier chapters. The hypotheses tested were that *A. dealbata* contributes substantially to

water use only in very young stands and that the productivity of *E. nitens* is not reduced by competition for water with *A. dealbata*.

6.2 Materials and methods

6.5.1 Site description

Six experimental plots were used for transpiration measurements, three in the earliest (1988, 8-year-old) planting on ex-pastures sites (Site 1; Plots A and B and Site 2; Plot J) and three in the most recent (1992, 4-year-old) planting on cleared native forest sites (Site 4;Plots T, U and V). *A. dealbata* was removed from Plots A and E in September 1995 (see Chapter 2 for full Site and Plot descriptions).

6.2.2 Transpiration Measurements

Twelve sapflow sensor units (Greenspan Technology, Warwick, Queensland) were used. One eucalypt (EucREF) and one acacia (AcREF) (both dominant trees), growing 2 m apart in Plot B, were used as reference trees in the manner described by Vertessy et al. (1995). These trees occupied similar canopy positions, exhibited crown form typical of the species at the site and exhibited no crown damage. They were measured for 30 days between 14/12/96 and 20/1/97.

Roving sensors were employed to make measurements on 3-4 trees in each of the six plots for a minimum of 4 days per tree. Two probesets (1 logger) were used on each tree for routine measurements, Probeset 1 in the northerly face of the tree, Probeset 2 in the easterly face. Thermistor pairs were placed at 10 mm and 5 mm depths under the cambium. Heat pulse was applied for 1.6 seconds at a frequency of ten minutes. Probes were implanted at a height of 1-1.5 m above the ground, below any live branches and vertically not within 15 cm of any deformation or wound in the stem. Probesets were moved regularly in all but the reference trees where they were reinstalled after 28 days.

Measurements of mean daily sapflux from trees using the roving sensors were regressed against measurements from the reference trees to predict daily water use for all trees for the entire sampling period (*sensu* Vertessy et al. 1995).

During this measurement period, soils at the 8-year-old site developed average deficits of 20 mm in the top 75 cm of the profile after initially being close to field capacity. Mean daily maximum and minimum temperatures were 21.0 ^{0}C and 6.3 ^{0}C respectively; mean daily vapour pressure deficit was 0.72 kPa and 11 mm of rainfall was recorded.

6.2.3 Radial variation

Radial variation in the conductivity of sapwood was accounted for by using a method modified from Daoqun et al. (1996). At the completion of routine measurements, radial profiles of sapflow for each sample tree were obtained on warm clear days. Daoqun et al. (1996) recommended that profile sampling across multiple axes was not necessary to obtain an accurate average sap velocity in *E. globulus*. Therefore, the above method was modified by reducing the number of moving probes from two to one in the determination of radial variation in sap velocity for each tree. Radial profiles in the southern axis were used with point measurements in the northern and eastern axes to determine correction coefficients (a simple weighted average of the sapflow ratios with depth in the sapwood) for each tree. The correction coefficients were applied to routine point measurements made 10 mm under the cambium (on two axes) to give an accurate estimate of sap velocity. Sapflow velocities were multiplied by sapwood area to compute sapflux in individual trees.

6.2.4 Stand transpiration

Mean daily sapflux values were used to develop linear regression relationships between sap flux and diameter at breast height over bark (*d*) for acacias and eucalypts in the 8-year-old stands. Similar relationships were developed in the 4-year-old stand. These

relationships were applied to diameter data collected in six 8-year-old plots (192 m^2) and a single 4-year-old plot (144 m^2) (referred to as plots 1-6 and plot 7, respectively) to estimate transpiration on a plot basis. For the mixed plots, it was necessary to combine eucalypt data for plots A and B and acacia data for plots B and U.

Regression relationships were also developed between plot transpiration and plot basal area of *A. dealbata* and plot transpiration and the ratio of plot basal area of *A. dealbata* to total plot basal area .

6.2.5 Sapwood area and volume fraction

At the completion of the measurement period, samples of wood were taken from all trees with an increment corer (5 mm diameter) for determination of sapwood radius (r_{sw}). Sapwood was identified by a yellow to red colour change of heartwood following application of dimethyl yellow. Sapwood area (A_{sw}) was calculated from d, bark depth and r_{sw} as determined from the core. Unstained sapwood segments from the cores were used for gravimetric determination of the volume fractions of wood, water and air for each sample tree.

6.3 Results

6.3.1 Sapwood characteristics

Sapwood area varied from 33.7 to 266.5 cm^2 for *E. nitens* and from 6.0 to 130.6 cm^2 for *A. dealbata* (Table 6.1). The sapwood/heartwood boundary was not as clearly defined in *A. dealbata* as in *E. nitens* primarily because of unassociated changes in wood texture in the former.

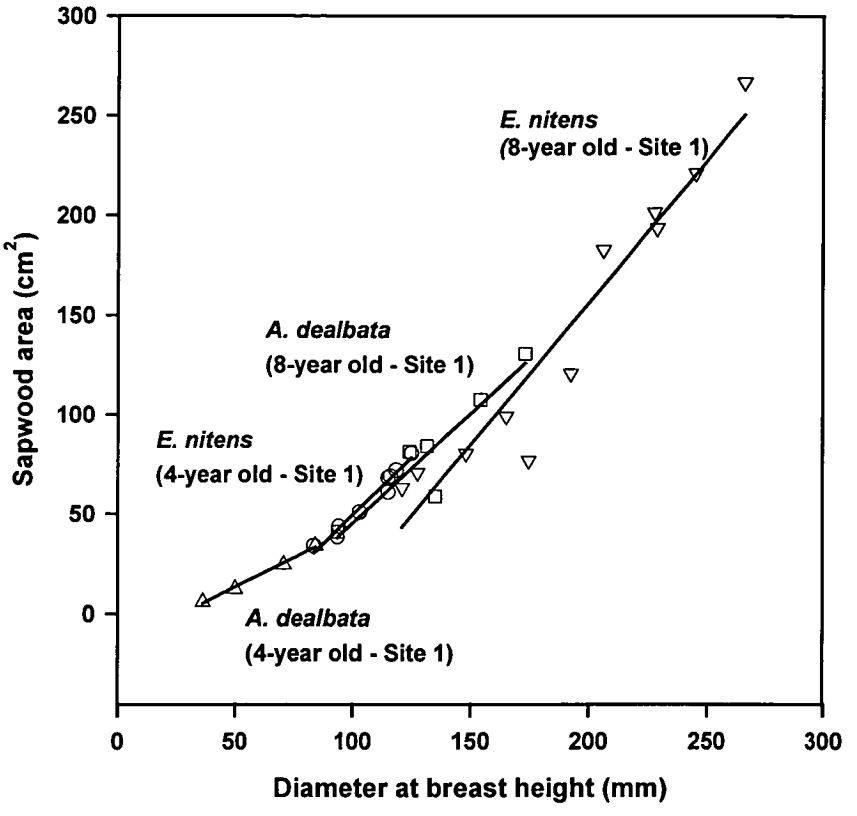


Figure 6.1. First order linear regression relationships between sapwood area and diameter at breast height over bark for 4-year-old and 8-year-old *A. dealbata* and *E. nitens* (8year-old *E. nitens* y=1.4x-129.5, r^2=0.92; 4-year-old *E. nitens* y=1.1x-65, r^2=0.97; 8-year-old *A. dealbata* y=1.1x-65.2, r^2=0.85; 4-year-old *A. dealbata* y=0.6x-15.8, r^2=0.99). Data from both *Acacia* infested and *Acacia* free plots were pooled for the eucalypt relationships.

Stem diameter explained 93% of the variability in sapwood area for both species (Figure 6.1). The relationships were stronger for 4-year-old trees (r^2 = 0.97 and 0.99) than for 8-year-old trees (r^2 = 0.92 and 0.85) for eucalypts and acacias, respectively (Figure 6.1).

Volume fractions of wood (V_w) and water (V_h) for *E. nitens* ranged from 0.27 to 0.38 and 0.48 to 0.67 respectively (Table 6.1) with no significant difference between sites or ages. For *A. dealbata*, the same variables ranged from 0.25 to 0.35 and 0.16 to 0.43 with a significant difference between *A. dealbata* ages and between species (p<0.05 in both cases).

Table 6.1 Stem diameter and sapwood parameters for sample trees. EucREF and AcREF are the reference trees.

Tree ID	*dbh* (mm)	Sapwood area (cm^2)	Sapwood radius (mm)	Vol. Fract. water V_h	Vol. Fract. wood V_w
***E. nitens* 8-year-old (Site 1)**					
E1	245	220.9	37.0	0.62	0.33
E2	121	62.9	22.0	0.60	0.29
EucREF	175	76.7	17.0	0.63	0.30
E4	128	70.5	24.0	0.62	0.32
E5	193	120.6	25.0	0.62	0.33
E6	165	99.0	25.0	0.62	0.32
E7	148	80.2	22.0	0.67	0.35
E8	229	193.4	34.0	0.57	0.35
E9	206	182.6	37.0	0.61	0.35
E10	228	201.4	36.0	0.62	0.33
E20	266	266.5	40.0	0.56	0.38
***E. nitens* 4-year-old (Site 4/Plot U)**					
E11	84	33.7	19.0	0.61	0.30
E12	94	43.6	21.5	0.60	0.33
E13	103	50.6	23.0	0.60	0.32
E14	94	38.2	18.0	0.60	0.32
E15	115	60.7	23.0	0.67	0.27
E16	119	71.7	27.5	0.62	0.29
E17	116	68.7	27.0	0.62	0.31
E18	115	67.9	27.0	0.58	0.34
E19	125	80.2	29.0	0.48	0.32
***A. dealbata* 8-year-old (Site 1)**					
A1	173	130.6	31.0	0.34	0.31
A2	135	58.8	17.0	0.43	0.32
A3	124	81.1	30.0	0.26	0.33
A4	132	84.0	28.0	0.40	0.35
A5	94	40.9	19.0	0.31	0.23
AcREF	154	107.5	30.0	0.27	0.29
***A. dealbata* 4-year-old (Site 4/Plot U)**					
A21	36	6.0	8.0	0.16	0.25
A22	50	12.5	11.5	0.18	0.29
A23	71	24.5	16.0	0.21	0.31
A24	84	34.0	19.0	0.20	0.28

6.3.2 Radial variation in sap velocity

Maximum values of sap velocity were recorded between 5 and 15 mm under the cambium in all trees. Axial variation in the sap velocity profile was observed. It was minimal in the absence of acacias (Plots J and T), but pronounced in mixed acacia/eucalypt plots (Plots B and U). Attempts to correlate axial variation with aspect were unsuccessful.

Sap velocity was predominantly but not always greatest on the northern axis. Correction coefficients that were developed from radial profile analysis (eg Figure 6.2) and subsequently applied to point data varied between 0.67 and 1.42 for the acacias and between 0.58 and 1.21 for the eucalypts, but were within 10% of unity for half of the 30 trees investigated. Eucalypts with similar sapwood areas returned almost identical correction coefficients. However, there was not sufficient replication to make a quantitative assessment of this observation.

6.3.3 Tree transpiration

Mean daily sapflux for EucREF varied between 4.5 and 17.7 l day^{-1} (mean 12.2 l day^{-1}), whereas for AcREF the mean daily sapflux value was 6.9 l day^{-1} (range 3.7 to 9.1 l day^{-1}) (Table 6.2). Sap velocities (data not shown) were very similar for the two trees. Although daily transpiration for AcREF was only half that of EucREF on most measurement days (Figure 6.3a), the two trees followed the same pattern of variation (Figure 6.3b). On heavily overcast days, the ratio of EucREF:AcREF transpiration was reduced.

First-order linear regression analysis of daily sapflux between EucREF and experimental trees yielded significant relationships ($p<0.05$) for all 8-year-old eucalypts except tree E2 ($r^2=0.81$, significant at $r^2=0.811$) (Table 6.2). Transpiration data for E2 were retained for subsequent analyses. Mean daily transpiration ranged from 5 l to 104 l (Table 6.2). There were no significant regression relationships between EucREF and 4-year-old eucalypts

(p>0.05). Consequently, E12 - E16 were regressed against E11 with significant relationships in all cases (Table 6.2). As Plot T eucalypts were not measured concurrently with other 4-year-old trees, they could not be used to estimate plot transpiration.

There were also significant linear relationships between daily transpiration of AcREF and that of other 8-year-old acacias (Table 6.2) but not 4-year-old acacias (r^2<0.1). Therefore, A24 was used as a reference tree for 4-year-old acacias (Table 6.2).

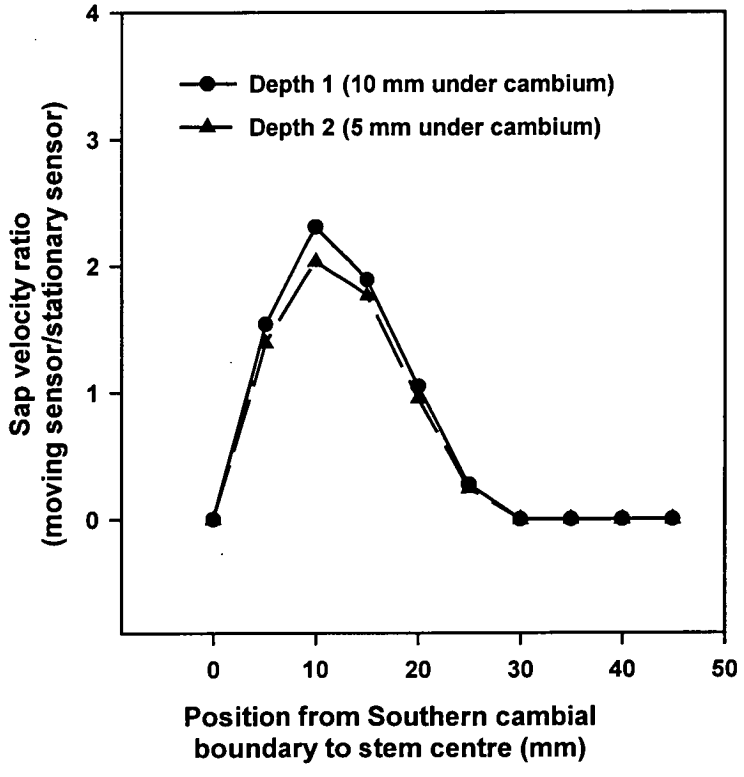


Figure 6.2. A typical profile of sap velocity ratio for a single radius (in this case a 4-year-old *E. nitens* in an *Acacia* infested plot). The stationary sensor was placed in the northern axis of the stem. The moving sensor sampled a profile on the southern axis.

Table 6.2 Sapflow parameters for sample trees (r^2 values refer to first order linear regressions between reference trees and experimental trees). The reference tree used for each species and age class combination is indicated in bold type.

Tree ID	Measurement days	r^2	Mean sapflux (l day^{-1})
***E. nitens* 8-year-old (Site 1)**			
E1	5	0.99	36.33
E2	5	0.81	5.01
EucREF	**30**	-	12.24
E5	8	0.73	38.52
E6	8	0.84	18.22
E7	8	0.89	19.00
E8	14	0.82	44.69
E9	11	0.98	103.57
E10	11	0.94	31.24
***E. nitens* 4-year-old (Site 4/Plot U)**			
E11	**15**	-	1.40
E12	14	0.96	9.08
E13	16	0.57	10.10
E14	6	0.84	18.15
E15	6	0.96	11.24
E16	6	0.97	17.38
***A. dealbata* 8-year-old (Site 1)**			
AcREF	**30**	-	6.90
A2	23	0.61	6.88
A4	5	0.83	8.42
A5	8	0.67	0.59
***A. dealbata* 4-year-old (Site 4/Plot U)**			
A21	5	0.95	0.26
A22	5	0.93	0.02
A23	6	0.97	2.04
A24	**16**	-	2.18

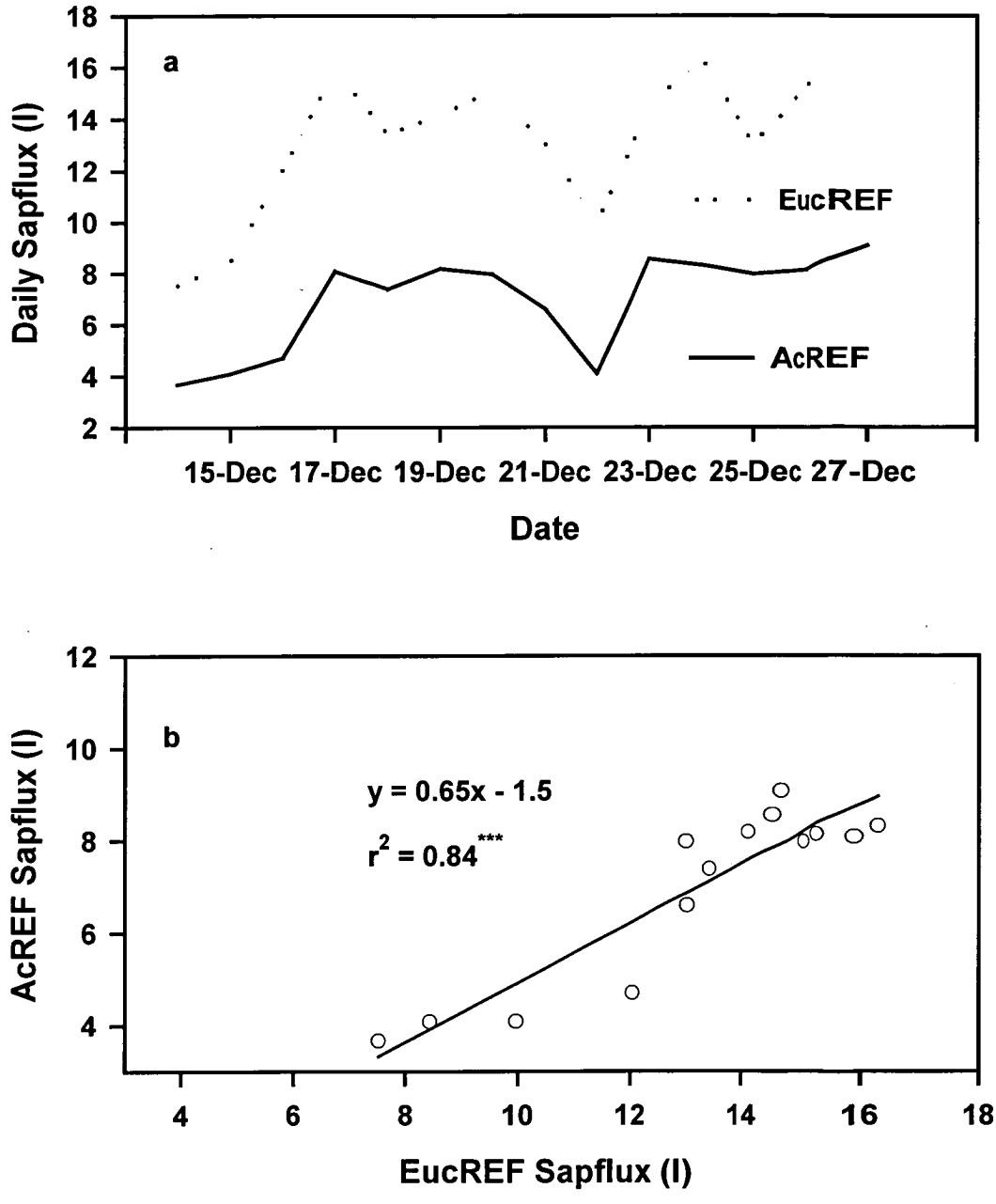


Figure 6.3. Relationship between daily sapflux of the reference *E. nitens* (EucREF) and reference *A. dealbata* (AcREF): (a) the pattern of variation between the two trees over a 14 day period in summer; and (b) the first order linear regression relationship describing the variation over the same period.

6.3.4 Plot transpiration

Eucalypts in the cleared plots (A and V) did not yield significantly different results from the corresponding competing plots (B and U). Therefore, eucalypt data were combined for plots A and B, and V and U, respectively, yielding significant regression relationships between *d* and mean daily sapflux in both cases (Figure 6.4a). The loss of one of only three replicates in plot J precluded any analysis of that plot. A significant regression relationship was obtained for mean daily sapflux and *d* for 4-year-old acacias (Figure 6.4a) but not for 8-year-old acacias. When all data for the two species were pooled, highly significant regression relationships were derived (Figure 6.4b).

Acacia dealbata contributed nearly half the water use in the 4-year-old plot (0.41 mm day^{-1}) and a mean value of 13% of water use in the 8-year-old plots (0.26 mm day^{-1}) (Table 6.3).

Significant curvilinear relationships between plot transpiration and either plot basal area of *A. dealbata* (Figure 6.5a) or the contribution of *A. dealbata* to total plot basal area (Figure 6.5b) indicated that increasing acacia basal area resulted in lower plot transpiration.

Table 6.3. Plot biometric characteristics and estimate daily transpiration

Plot ID	Age (Yr)	Transpiration (mm)	*A. dealbata* contribution (%)	*A. dealbata* frequency (stems ha^{-1})	*A. dealbata* basal area m^{2}ha^{-1}	*E. nitens* basal area m^{2}ha^{-1}
Site 1						
B	8	2.0	9	2407	13.6	21.9
C	8	2.3	9	1296	10.0	23.8
F	8	2.8	24	2130	7.4	23.3
G	8	1.4	9	5648	13.5	15.6
H	8	1.6	16	3796	17.9	15.1
I	8	2.0	12	2593	13.9	18.3

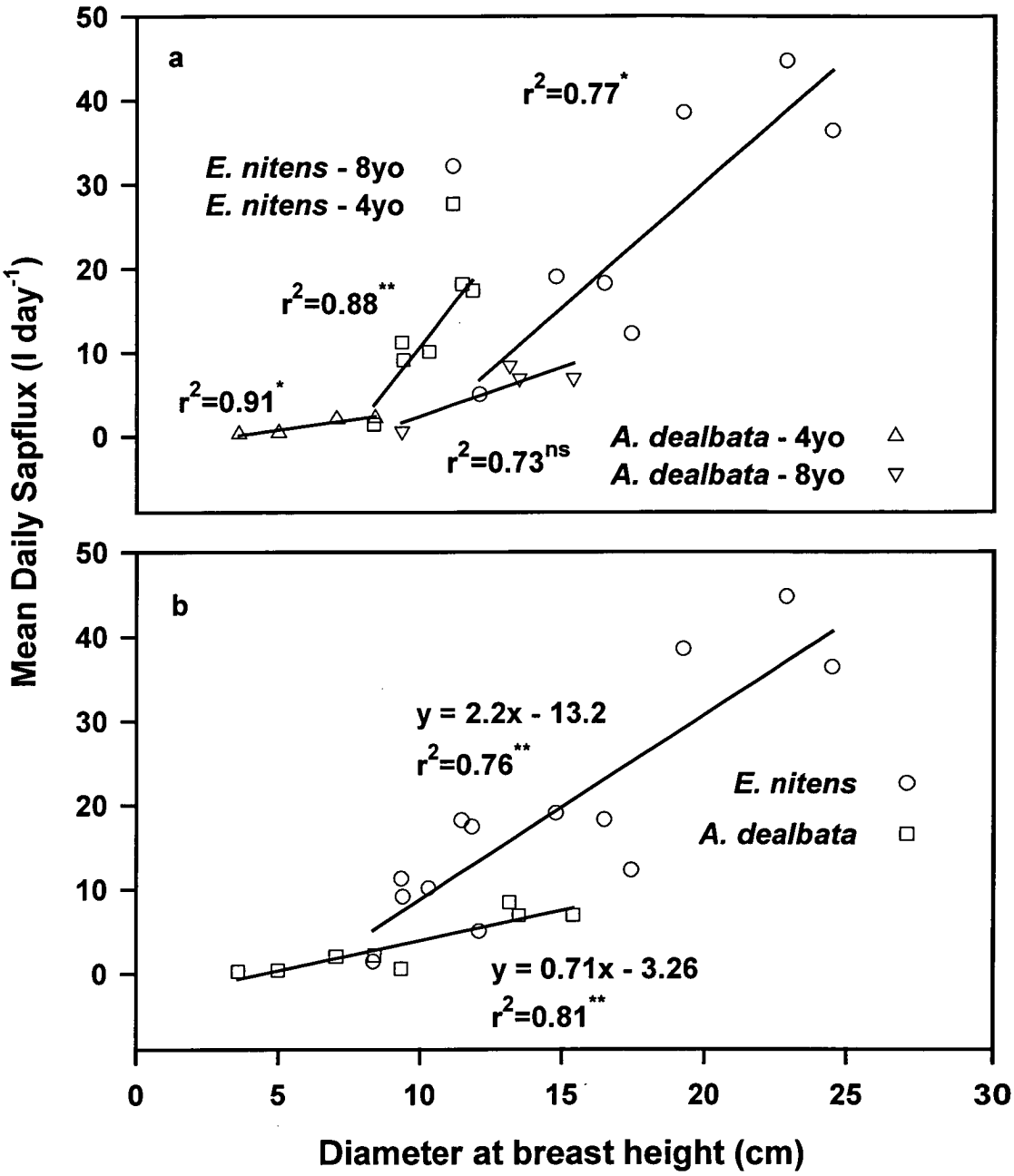


Figure 6.4. First order linear regressions describing the relationships between estimated mean daily sap flux and diameter at breast height: (a) for 8-year-old and 4-year-old *A. dealbata* and *E. nitens*; and (b) for *A. dealbata* and *E. nitens*, ages combined.

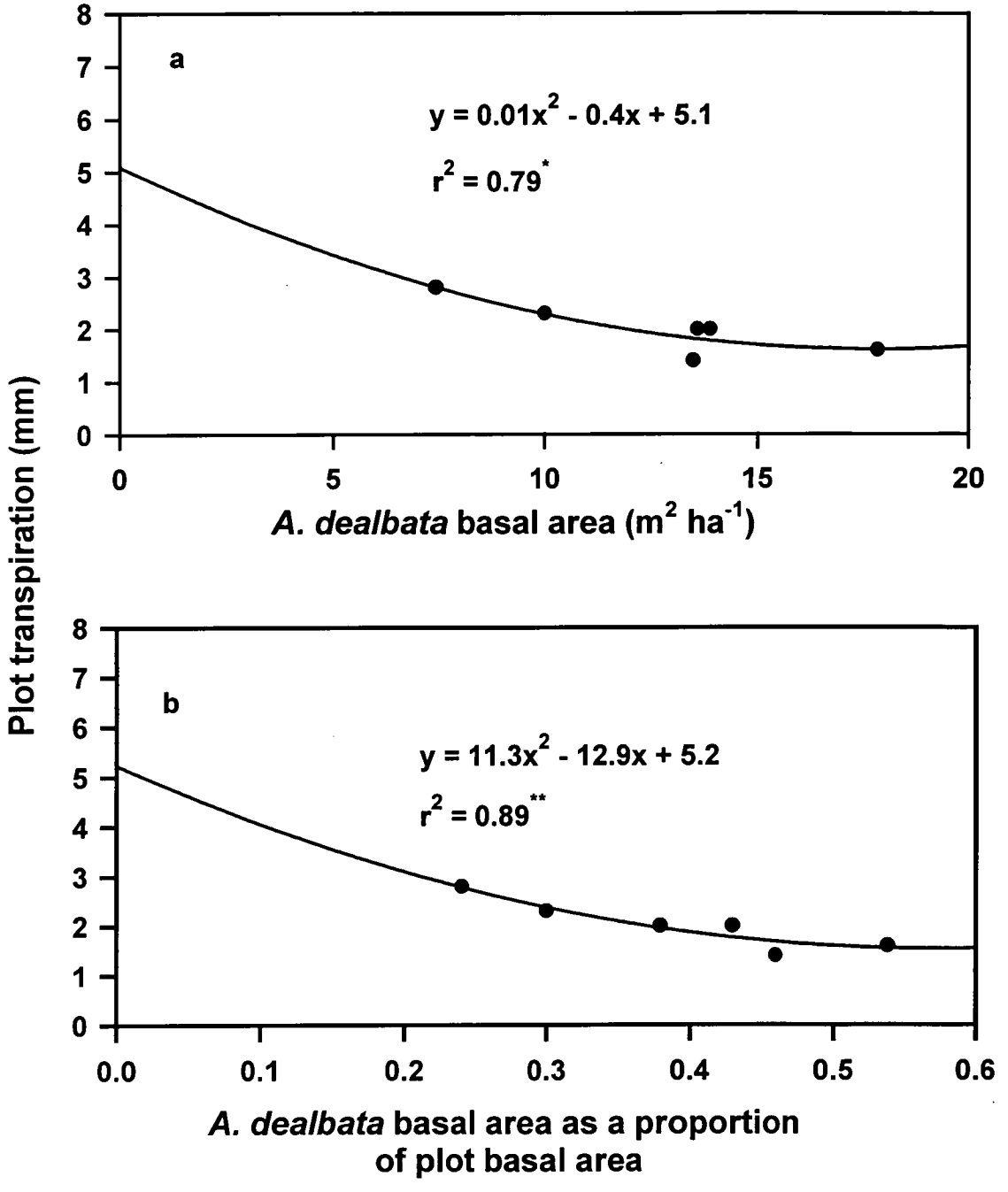


Figure 6.5. Second order linear regression relationships describing the influence of *A. dealbata* infestation on plot transpiration in terms of: (a) absolute *A. dealbata* basal area and; (b) the proportional contribution of *A. dealbata* basal area to plot basal area for the six Site1 8-year-old plots.

6.4 Discussion

Acacia dealbata contributed significantly to stand water use at the experimental site. The contribution was proportionally greater in 4-year-old stands than in 8-year-old stands. In stands of both ages, plot water use (1-3 mm day^{-1}) was less than would be expected for a closed eucalypt canopy (Honeysett et al. 1992). The amount of *A. dealbata* infestation was associated with absolute plot water use and regression models predicted that in the absence of acacia competition plot water use would approach 5-6 mm day^{-1} during the growing season (Figure 6.5).

The distribution of sapwood area data reflect the dominant canopy positions of eucalypts in mixed plots of both ages. The largest acacias considered in 8-year-old and 4-year-old stands possessed sapwood areas of only 60% and 70% respectively compared to their eucalypt counterparts. Because of soil and tree heterogeneity at a local scale the selection of trees for scaling of water flux to the stand level is difficult (Kostner et al. 1996) even in plantation monoculture. However, in the present study of a mixed species stand, stem diameter was demonstrated to be a suitable inventory parameter for scaling transpiration measurements from tree to stand level. Similarly strong relationships have been reported both for conifers (Cermak and Kucera 1987) and eucalypts (Vertessy et al. 1995; Hatton et al. 1995. The strong relationships between *d* and sapwood area reflect those derived by Vertessy et al (1995) in a similar study of *Eucalyptus regnans* and *A. dealbata* in a mixed native forest. Closer relationships in younger trees are likely to reflect changes in dominance occurring between ages 4 and 8 years. As vigorously growing trees are suppressed by their neighbours, reduced access to light will result in a decline in leaf area and water use and subsequently in stem conducting area. 8-year-old acacias were predominantly suppressed trees. Hence, the relationship was weaker for these trees than the eucalypts. The stronger relationship between the two parameters for acacias than eucalypts

in the four year old stand reflects the larger size of the dominant eucalypts and greater formation of heartwood. In the acacias, heartwood formation has either not occurred or is minimal.

In some 4-year-old eucalypts, the radial profile of sap velocity implied sapflux beyond the sapwood/heartwood boundary clearly indicated by core staining. This resulted in discrepancies in sapwood area determination of up to 30%. Although consequent differences in computed sapflux values were small (as the sap velocities returned in the disputed area were themselves low compared to those in the periphery of the sapwood), they may provide a significant source of error in scaling exercises. The capacity for the Greenspan system to discriminate between low sap velocities and the absence of sapflow has been identified previously (Becker 1996). In the present study a timeout value of 150 seconds was imposed (ie. an error record occurred if the heat pulse was not recorded at both sensors within 150 seconds of the signal being sent). Nevertheless, low values still required cautious interpretation. When determining sapwood area from cores, a light diffraction method (as opposed to staining) as used by Vertessy et al. (1995) is perhaps necessary for achieving a sufficiently accurate value to confidently impose on sap velocity measurements.

Sapwood characteristics were dominated by the species differences in V_h. Whilst different values among species have been noted elsewhere, their possible implications for water use have not been inferred. The difference in V_h between acacia age classes may indicate water stress in the younger trees. Such a relationship has been noted for *Eucalyptus globulus* (D. White, personal communication). The shallower soil profile and sloping terrain associated with the 4-year-old stand support this hypothesis. If this is the case, the inference is that eucalypts of neither stand were drought stressed when sampled at the end of the experimental period.

Radial variation (from the centre to the periphery of the stem) in sapflow velocity followed similar patterns for the two species and was higher at the periphery of the sapwood as has been reported in other studies for a variety of species (eg Swanson 1967; Swanson 1974; Daoqun et al. 1996). Cyclic variation in sap velocity within radii, which has been reported in several studies (eg Dye et al. 1991), was not observed for either species. Axial variation in sap velocity (planar variation within an annulus) has been reported in Douglas-fir (Cohen et al. 1985) and in that study was not associated with changes in sun position. Uneven axial distribution of crowns about the stem in the present study is therefore likely to have strongly influenced the axial variation in sap velocity of trees in mixed plots. As it was not possible to quantify three-dimensional crown distribution in the experimental trees (and thereby adjust the sampling protocol), a significant source of error potentially exists. Therefore, more rigorous sampling may be required for determination of a sap velocity correction coefficient under mixed species conditions than in monoculture. In the present study, where cyclic variation in the sap velocity profile was not observed, concurrent point measurements in the 5-15 mm annulus at the four cardinal radii is probably sufficient to reduce potential errors to an acceptable level (when combined with a full profile on a single radius). However, a full error analysis is warranted for future studies, and particularly in species where cyclic radial variation has been reported (e.g., *Eucalyptus regnans*; Dunn and Connor 1993).

For trees occupying the same canopy position, species differences in tree transpiration were primarily due to differences in sapwood area and the time during which sap velocities were at or close to the maximum, rather than any significant differences in maximum sap velocity. However, subdominant and suppressed trees (generally acacias) exhibited significantly ($p<0.05$, t-test) lower sap velocities than dominant neighbours in either 4-year-old or 8-year-old stands. For such trees, limited light availability was likely to have

been responsible for lower maximum sap velocities and shorter periods of high sap velocities. The role of shading has been previously put forward as a reason for higher variation of sap flux among trees (Diawara et al. 1991). In studies where trees have been widely spaced, between-tree variation has been low (Granier et al. 1990; Loustau et al. 1996) whereas in closed forest canopies variability has been high (Kelliher et al. 1992; Kostner et al. 1992). Between tree variation in mean daily sapflux is related to social position within stands (Kelliher et al. 1992). In a *Nothofagus* forest, Kostner et al. (1992) reported that 50% of plot sap flux came from 3 of 14 trees which were emergent and that significant differences existed in sap flux density between canopy layers. Granier (1987) similarly reported variation in sapflux density among dominance classes in Douglas-fir as did Teskey and Sheriff (1996) for *Pinus radiata.* Although such differences among trees, which reached an order of magnitude within plots in the present study, are predominantly driven by light, the frequency of gust penetration has also been put forward as a possible contributor (Kelliher et al. 1992).

The decrease in EucRef:AcRef sapflux ratio on overcast days resulted from proportionally greater decrease in eucalypt water use than increase in acacia water use. Homogenisation of the radiation environment may have contributed to this result. Different leaf level responses to atmospheric conditions are also likely to be involved and these are considered in the following chapter.

Plot transpiration estimates were within the range expected for a native eucalypt forest (0.81-1.86 mm day^{-1} Dunn and Connor 1993; 2.9 mm day^{-1} Vertessy et al. 1995), a coniferous forest (0.67 mm day^{-1} Cermak et al. 1995) or a pine plantation (1-5 mm day^{-1} Whitehead and Kelliher 1991) but less than half that expected for a closed canopy eucalypt plantation (5-6 mm day^{-1} Honeysett et al. 1992). There was no indication of drought stress as a mechanism for the twofold discrepancy between expected and estimated plot

transpiration. The regression relationships in Figure 6.5 indicated that plot water use would approach the expected value of 5-6 mm day^{-1} in the absence of acacia competition. It follows, therefore, that (a) *A. dealbata* is not limiting the water available to *E. nitens* in the 8 year-old plantation, and (b) *A. dealbata* is restricting the water use (and by definition the productivity) of *E. nitens* through competition for another limiting resource which drives water use. These results support those from Chapter 4 indicating that light is the primary limiting resource for *E. nitens.* The suppressed water use that results from the mixed canopy structure indicates that *A. dealbata* may respond differently than *E. nitens* to atmospheric weather variables and/or soil moisture availability. However, plot water use for monocultures of *A. mearnsii* (a species very similar to *A. dealbata*) have been observed elsewhere to reach 5 mm day^{-1} (P. Dye, pers. comm.). It is therefore unlikely that a monoculture of *A. dealbata* would exhibit the same plot water use as observed for that species in the present polyculture system. Therefore, the dual species nature of the plantation in this study may in itself be an important determinant of the water use of *A. dealbata.* Additionally (or alternatively) intraspecific competition among *Acacia* stems may affect root/shoot ratios to an extent that restricts the access of individual *A. dealbata* stems to the soil water resource. Accordingly, physiological and morphological aspects of behaviour and competition at the leaf level are considered in the following chapter.

Chapter 7. Foliar gas exchange and plant water status

7.1 Introduction

Results presented in the previous chapters have indicated that *A. dealbata* significantly competes with *E. nitens* in young plantations and that the primary limiting resource for *E. nitens* is light. By age 8 years, most *A. dealbata* stems have been suppressed in the mixed canopy and it is likely that surviving individuals will ultimately persist only in the understorey. As stated in Chapter 4, competitive outcomes are determined by the capacity of individuals to capture, utilise and allocate resources. Resource allocation, as well as associated plant morphology at the canopy and crown scale, has been considered in previous chapters. In this chapter, resource capture and use are considered at the leaf level, primarily from a physiological rather than a morphological perspective.

Elsewhere in this thesis it was established that in a 4-year-old *Acacia*-infested stand, *A. dealbata* contributed nearly half of LAI and a similar proportion of water use (refer to Chapters 4 and 6 respectively). However, in 8-year-old *Acacia*-infested stands, *A. dealbata* contributed 20% of LAI but only 13% of water use. Whilst lack of statistical validity limits the comparison, two clear trends are evident. Firstly, *A. dealbata* is declining in its contribution to plot LAI. Secondly, the relative contribution that *Acacia* makes to plot water use is declining faster than its relative contribution to plot LAI. Of particular interest in the context of this thesis are the mechanisms that reduce the competitiveness of *A. dealbata* at or soon after canopy closure.

During the period of growth up to canopy closure *A. dealbata* foliage coexists with *E. nitens* foliage. Therefore, the placement of above-ground plant parts and the associated ability to intercept radiation is unlikely to be an important factor at this stage. Based on this assumption, the mechanism for interspecific competitive superiority is likely to be related

to relative access to (and use of) water and relative photosynthetic capacity. Should *A. dealbata* exhibit a lower maximum photosynthetic rate than *E. nitens*, or be less able to realise high photosynthetic rates due to limiting water availability in the soil (indicated by predawn leaf water potential) and consequent reduction in stomatal conductance, a competitive advantage would be gained by *E. nitens*. During the early stages of stand growth, such a disadvantage for *A. dealbata* could be masked by preferential allocation of photosynthate to above ground resources, or the possible non-limiting nature of light and water in the young stand. Neither scenario would be sustainable in the long term as increased water use exceeded the capacity of a comparatively reduced root system, or as resources became limiting under the greater demand of the larger, older canopy.

E. nitens has been the subject of two detailed gas-exchange studies (White 1996; Pinkard 1997) but the physiology of pinnate *Acacia* species has received only limited attention (eg Roux and Middlemiss 1963; Brodribb and Hill 1993). Comparative studies of eucalypts and co-existing pinnate species are absent from the literature. Indeed, comparative studies of codominant tree species have been largely restricted to northern hemisphere conifers and deciduous broadleafed trees, (eg Shainsky and Radosevich 1992) and complex rainforest communities (eg Myers *et al.* 1987).

A full investigation of *A. dealbata* autecology, which is necessary for a complete assessment of the comparative foliar physiology of the two species, was a task beyond the scope of the present study. Nevertheless, a small experimental program was undertaken to test the following hypotheses in the field.

1. *E. nitens* foliage has a higher photosynthetic capacity than *A. dealbata.*

2. *A. dealbata* foliage is more water limited (on a diurnal basis) than *E. nitens*.

7.2 Materials and Methods

7.2.1 Site description

The primary study site was established in mid 1994 in the 1988-planted coupe of *E. nitens* on the ex-pasture site at the valley floor (Site 1). *A. dealbata* was present as an understorey and co-dominant weed in large numbers. A 25 m tall scaffolding tower (2.4 m x 2.4 m at the base) was erected at the site (in Plot B) to facilitate access to the forest canopy for leaf level physiological measurements (Figure 7.1). The tower was sited in a small canopy gap at a location considered to typify local stand structure and so as to give access to sufficient tree crowns to enable replication of sampling. Six eucalypt crowns and eleven acacia crowns were accessible (Figure 7.2). Sites 2 and 4 were additionally used for measurements not requiring scaffolding for access to the canopy (see Chapter 1 for full site descriptions).

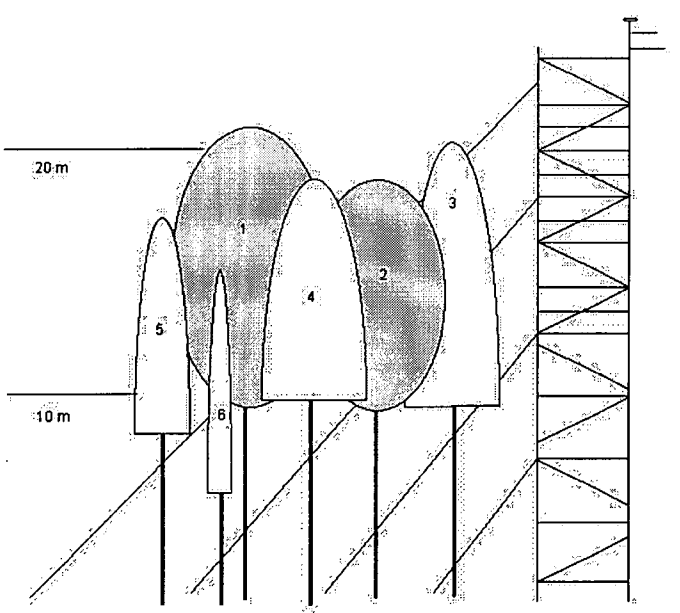


Figure 7.1. Canopy tower for gas exchange measurements at Site 1. Diagrammatically represented are *E. nitens* in 1. dominant/emergent and 2. co-dominant canopy positions and *A. dealbata* in 3. dominant; 4 co-dominant; 5. sub-dominant and 6. understorey canopy positions.

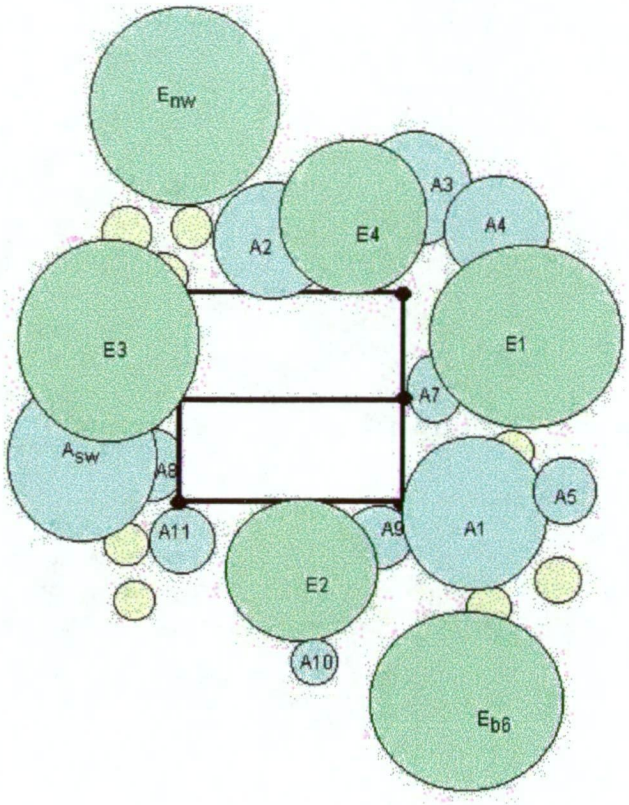


Figure 7.2. The position of trees sampled from the canopy tower. Unlabelled trees are understorey *A. dealbata* that were not included in the experiments.

7.2.2 Measurement of soil moisture

Soil moisture was measured using a neutron moisture meter (NMM, CPN503, Pacheco, California). Aluminium access tubes of 38 mm internal diameter were hand augered into the soil to a depth of 1.2 m - 2.5 m. At Site 1, nine access tubes were augered in 1994, three in each of three plots chosen to represent the site topography (Plots A, B and I – see Chapter 2). Each plot was divided into nine subplots, three each of which were chosen randomly for placement of the access tube. Tubes were placed as close to the centre of each subplot as possible. During winter 1995, a further eight tubes were augered. Two of these were deep tubes (> 2 m), the remaining five tubes reaching a depth of 1.6 m. Of the eight new tubes, three were located at Site 1 (deep tubes in Plots A and B, and an additional shallow tube in Plot A) and five at Site 2 (distributed in a cross pattern over

Plots J, K and L). Placement at Site 1 was chosen to enable fuller investigation of soil moisture conditions near the physiology plot (Plot B). At Site 2, placement was chosen to cover the site as completely as possible with the limited number of tubes.

Calibrations were obtained for the surface soil (0-0.125 m) and sub-surface soil (0.125 - 1.5 m) (Figure 7.3) (Worledge *et al.* 1998). Soil water content (θ_s) was measured at 0.15 m intervals down to 1.0 m and 0.3 m intervals thereafter. θ_s was calculated as total soil water content (mm).

Soil moisture measurements were generally made every week in the peak of the growing season, fortnightly during spring and autumn and less regularly during winter.

Additionally, rainfall data were collected from a nearby weather station (~ 5 km).

7.2.3 Measurement of leaf water potential

Leaf water potential (ψ) was measured using a Scholander-type pressure chamber (PMS Instruments, Coriallis, Oregon, U.S.A.). Following excision, leaves were normally placed within the chamber within one minute and measured within a further minute (after Turner, 1988). On some occasions it was more practical to gather up to five replicate leaves at once and these were immediately placed within a darkened ice-cooled insulated container where they remained until measurement for up to ten minutes. An estimate of the water status of a tree crown (or part thereof) was gained by measuring a minimum of three replicate leaves from different branches. Where results varied by more than 10% around the mean, a further 2-3 replicates were obtained. The diurnal course of ψ was measured in acacias and eucalypts at Site 1 on 13/2/96, 22/2/96, 8/3/96 and 13/3/96 and from pre-dawn until late afternoon on 24/2/96 and 17/1/97. Pre-dawn leaf water potential (ψ_{max}) measurements were

also made at Site 1 on four additional occasions 13/12/95, 17/12/95, 28/12/95 and 31/12/96. Pre-dawn measurements were made at Site 2 on 28/12/95 and 30/12/97 and at

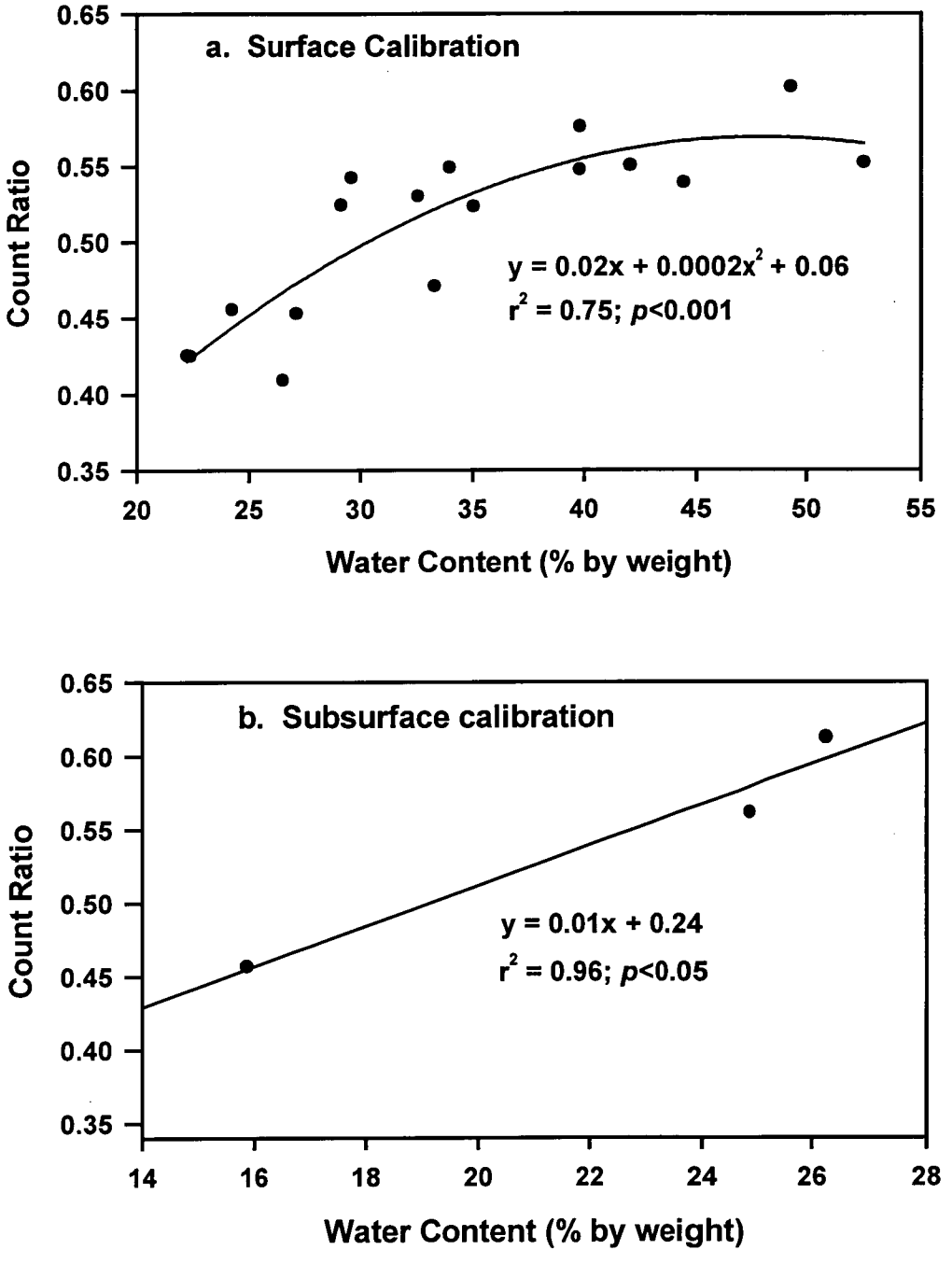


Figure 7.3 Soil moisture calibrations for the neutron moisture meter (NMM) for (a) surface soil (0 - 15 cm) and (b) subsurface soil (15 - 150 cm). Regression equations were applied to routine measurements with the NMM to provide estimates of soil water content.

Site 4 on 28/12/95 and 31/12/96. A series of measurements was made post-dusk at Site 4 on 14/1/97 and at Site 1 on 20/1/97 and 21/1/97.

7.2.4 Measurement of foliar gas exchange

Stomatal conductance (g_s) was measured using a Licor 1600c steady state water vapour porometer (Licor Inc., Nebraska, USA) with a 1 cm^2 sample aperture on the sensor head. Net CO_2 (A) and g_s were measured with a portable open gas analysis system incorporating an infrared gas analyser (LCA-2, Analytical Development Corp., Hoddesdon, Herts, U.K.). Neutral density filters were used in the cuvette of the instrument to control photosynthetic photon flux density (PPFD) incident at the leaf surface for the development of photosynthetic light response curves as was a quartz halogen artificial light source for the provision of constant PPFD. Both instruments were used to record microclimatic variables at the leaf surface including photosynthetic photon flux density (PPFD), relative humidity (h), leaf temperature (T_l) and cuvette temperature (T_c).

The diurnal course of g_s of acacias and eucalypts was measured with the porometer on three occasions at Site 1 - 13/2/96, 22/2/96 and 13/3/96. On two further occasions (24/2/96 and 17/1/97) measurements were made from dawn to mid-afternoon. The LCA-2 was used on four occasions, on 13/3/96 and 17/1/97 to follow the diurnal course of A and on 7/3/96 and 8/3/96 to determine single leaf light response curves and investigate within-crown variation in A. The light response curves were started at high PPFD with a two minute acclimation period prior to measurement following each PPFD reduction. Both species were considered on the four LCA-2 measurement days. On each tree, at each measurement time, a sample of five - ten replicate leaves was used for the porometer. The number of replicates was least when within-sample variation was small and largest when individual leaf responses were most variable. Three replicate leaves were sampled from each tree for the LCA-2 during diurnal measurements.

Unless otherwise stated, fully sunlit leaves from the upper third of the tree crown were used for all foliar measurements.

7.2.5 Data analysis

Physiological data obtained from each diurnal measurement series were graphed and examined visually for trends. All data derived from diurnal measurements were aggregated into a single data set for statistical analysis using the GLM module of SAS. Effects of date, time and weather variables on physiological response were considered. Additional effects of crown position on physiological variables were analysed using ANOVA.

Light response curve data obtained by the LCA-2 were similarly graphed and examined visually for trends. They were not included in the diurnal data set (above) for statistical analysis as they were obtained under imposed rather than ambient field conditions. t-tests were employed to investigate between-species responses to individual variables.

7.3 Results

7.3.1 Rainfall and soil moisture

The 1995/96 growing season was wetter than the 1996/97 season, with twice as much rain falling in the four months December - March (Table 7.1). Measurements of water potential and gas exchange on 17/12/95 were preceded by heavy rainfalls. However, only 15 mm of rain was recorded between 13/2/96 and 13/3/96. In 1996/97, following a fall of 12 mm on 10/12/96, no substantial rain fell until 9.5 mm on the eve of the final measurement day (17/1/97).

Soil moisture data were not reliable for the three access tubes in Plot I nor for a single tube each in Plots A and B. Hence these data were excluded from analyses. During December 1995, soils were generally below field capacity, particularly in the physiology plot (B-tubes) and in the *Acacia*-free 8-year-old plot (J-tubes) but less so where *A. dealbata* had

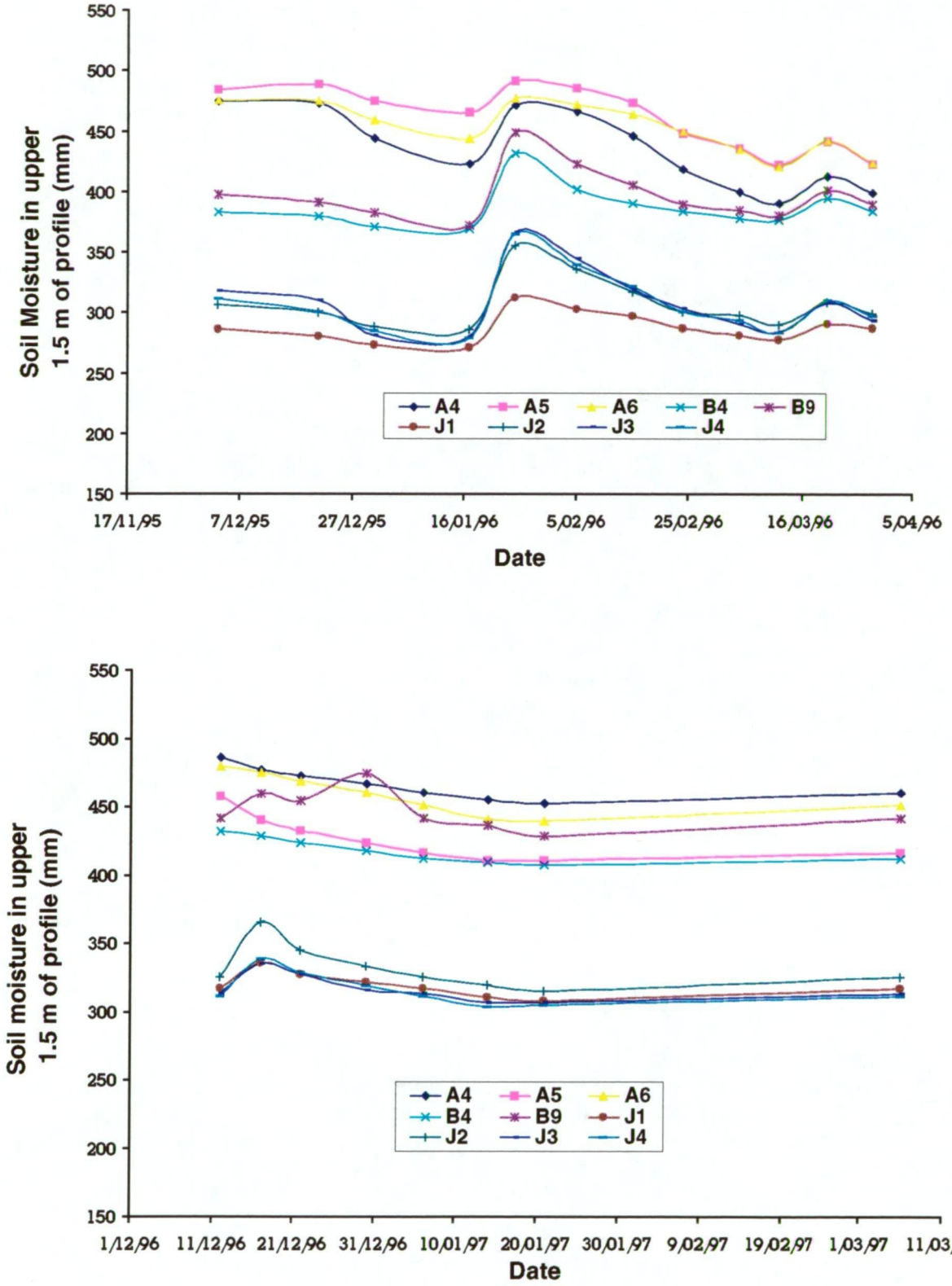


Figure 7.4 The seasonal course of soil moisture during (a) the 1995/96 growing season and (b) the 1996/97 growing season. Tubes identified with the prefix A were sited in Plot A (at Site 1) where competing *A. dealbata* had been removed. "B-tubes" were situated in the adjacent Plot B (at Site 1) where the canopy tower had been erected and physiological measurements were undertaken. "J-tubes were distributed about Site 2, where *A. dealbata* was absent.

been recently cleared (A-tubes) (Figure 7.4a). A substantial rainfall event in mid-January returned soils to field capacity prior to steady drying in all tubes as the growing season progressed.

In early December, 1996, the J-tubes indicated reduced soil moisture status, recovering in mid-December, before a gradual decline over the remainder of the period of measurement. Except for the deep tube in the physiology plot (B9), no improvement of soil moisture status was indicated in December for the other plots. Overall, soils gradually dried for the entire 1996/1997 sampling period but did not reach the December deficits of the previous year (Figure 7.4b).

Table 7.1 Rainfall summary (mm) for the years considered in the study

Year	1995	1996	1997
January	75.5	124.0	46.5
February	49.0	56.5	39.0
March	36.0	64.0	30.5
April	69.0	61.5	36.0
May	82.5	20.0	175.0
June	169.0	105.5	60.0
July	117.5	124.0	38.5
August	55.5	176.0	96.5
September	58.0	158.0	100.5
October	45.0	65.0	43.5
November	55.5	56.0	39.5
December	60.0	30.0	39.5
Total	**872.5**	**1040.0**	**745.0**

7.3.2 Leaf water potential

At Site 1, for codominant trees on days of moderate evaporative demand, ψ fell from pre-dawn maxima to minima in late morning. In both growing seasons, *E. nitens* generally

maintained pre-dawn values (ψ_{max}) of less than -0.5 MPa. However, ψ_{max} was significantly related ($p < 0.01$) to both species and measurement date. *E. nitens* returned less negative pre-dawn values than *A. dealbata* which was less able than *E. nitens* to return to maximum values of ψ_{max} after extended rain-free periods (eg on 8/3/96, Figure 7.5). There was no significant interaction between date and species in their effect on ψ_{max}, indicating that the two species responded in the same manner (but to a different extent) to declining soil moisture status. ψ_{max} for *E. nitens* at Site 2 remained greater than -0.6 MPa for all trees measured on both measurement days. At Site 4, ψ_{max} was variable for both species but no significant difference was apparent between them ($p > 0.05$; t-test). When the complete water potential data set was analysed (SAS GLM), species was not found to be

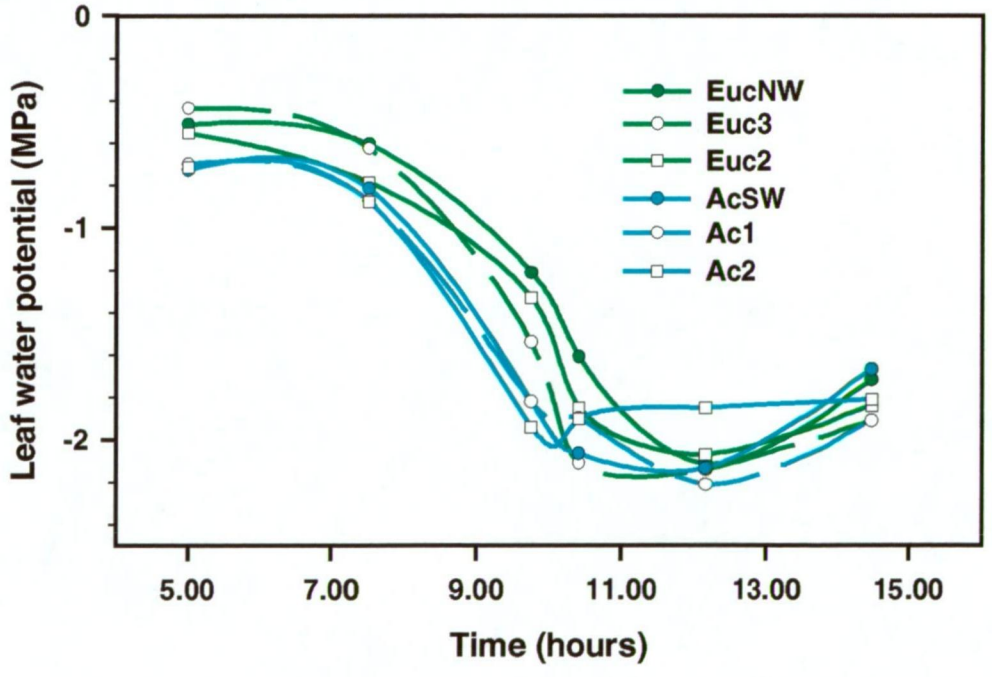


Figure 7.5 The diurnal course of leaf water potential measured with the pressure chamber on 8/3/96. Euc3, EucNW, AcSW and Ac1 were co-dominant trees. Euc2 and Ac2 were subdominant Upper crown foliage from each tree was sampled on six occasions throughout the day.

For *E. nitens*, there was no significant effect of crown position on ψ but a significant time effect ($p < 0.001$) and a significant interaction between the two ($p < 0.01$). That is, whilst the variation vertically within the crown was small, the water potential of upper crown foliage declined during the day to a greater extent than middle and lower crown foliage. Furthermore, upper and middle crown foliage of *E. nitens* was slower to recover during the afternoon than either lower crown foliage of that species or foliage from all crown zones of *A. dealbata* (e.g. Figure 7.6). For *A. dealbata*, differences among all of crown position, time, and their interaction were highly significant ($p < 0.001$). Dominant trees of the two species maintained higher afternoon ψ than subdominant trees on days of moderate evaporative demand and recovered sooner (eg 17/01/97, Figure 7.7).

At Site 1, ψ of both *A. dealbata* and *E. nitens* recovered rapidly after sunset, reaching pre-dawn values within approximately one hour. *E. nitens* recovered faster than *A. dealbata*, but not significantly so ($p > 0.05$, ANOVA, two factor with replication). At Site 4, post-dusk results were highly variable within all plots and no trends were evident.

7.3.3 Stomatal conductance

On 13/2/96, two distinct patterns of conductance were apparent (Figure 7.8). The dominant eucalypts had high g_s when first measured which declined markedly during the morning prior to a post-noon maximum and subsequent steep decline. In the two acacias (one dominant and one subdominant) and in the subdominant eucalypt, g_s rose initially to a mid-morning peak, declined at midday and recovered to a secondary peak in mid-afternoon, before finally declining again in late afternoon. Cloudiness and consequent reduction in incident PPFD were associated with the morning decline in g_s of the two dominant eucalypts. PPFD was not reduced during measurement of the other trees.

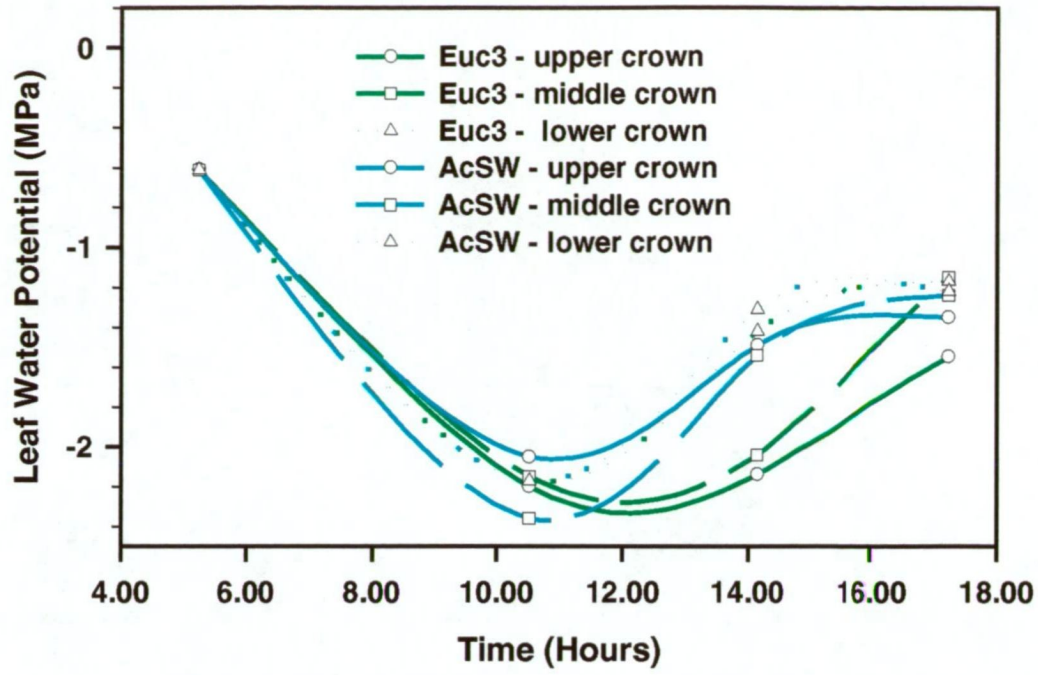


Figure 7.6 The diurnal course of leaf water potential measured with the pressure chamber on 13/2/96 for co-dominant *A. dealbata* and *E. nitens* (AcSW and Euc3 respectively). Leaves from upper. middle and lower crown zones were sampled from each tree on four occasions throughout the day.

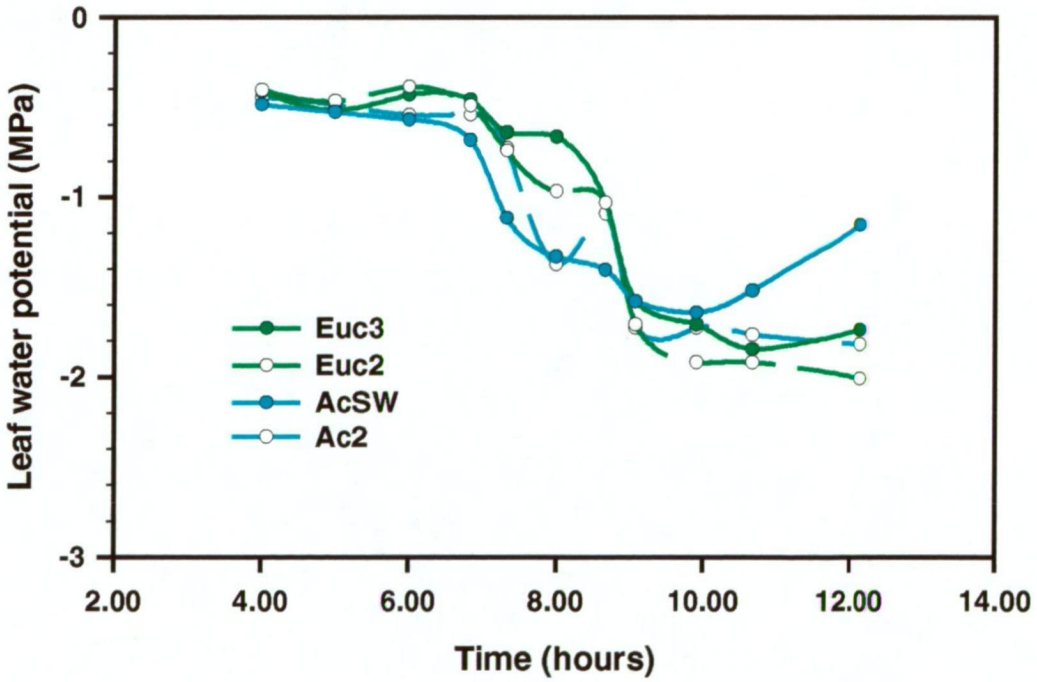


Figure 7.7 The diurnal course of leaf water potential measured with the pressure chamber on 17/1/97 for co-dominant and sub-dominant *A. dealbata* (AcSW and Ac2 respectively) and *E. nitens* (Euc3 and Euc2 respectively). Upper crown foliage was measured on eleven occasions throughout the day.

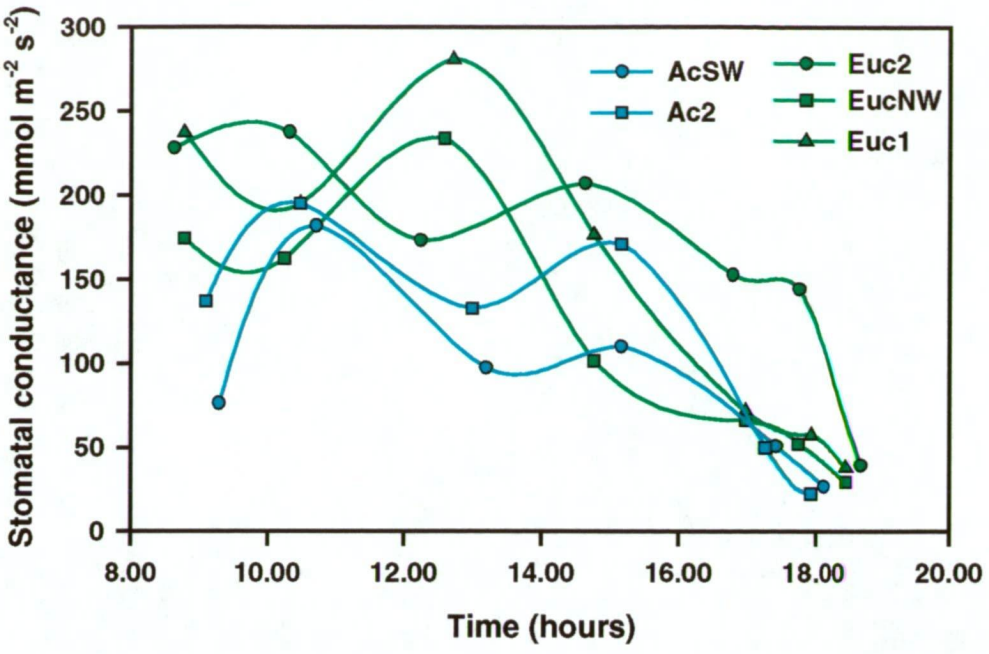


Figure 7.8 The diurnal course of stomatal conductance measured with the LI 1600 porometer on 13/2/96 for co-dominant and subdominant *A. dealbata* and *E. nitens*.

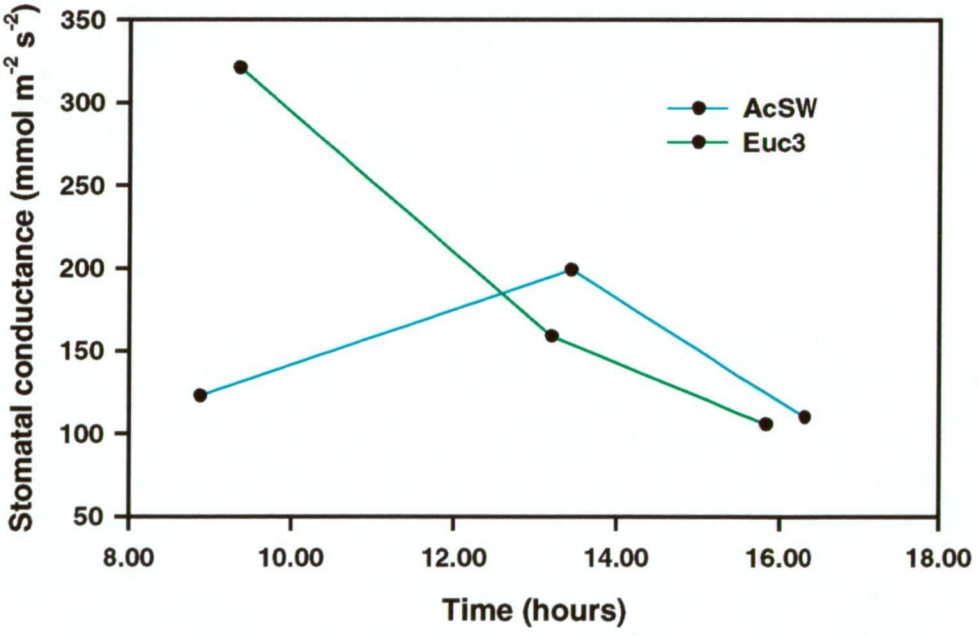


Figure 7.9 The diurnal course of stomatal conductance measured with the LI 1600 porometer on 13/3/96 for co-dominant *A. dealbata* and *E. nitens*.

On 13/3/96, the codominant acacia and eucalypt exhibited different patterns of variation in g_s (Figure 7.9). Wet leaves prevented measurement until both trees were fully sunlit. At the time of first measurement, the eucalypt had a maximum g_s of over 300 mmol m^{-2} s^{-1}. g_s declined to half this value at midday. However, g_s of *Acacia* rose from a low morning value to a midday maximum of 150 mmol m^{-2} s^{-1} before a subsequent decline.

Acacias of different dominance classes exhibited variation in the diurnal pattern of conductance on 22/2/96 (Figure 7.10). In shaded leaves of the dominant and understorey acacias and in both sunlit and shaded leaves of the subdominant tree, morning maxima in g_s were followed by decline towards midday and recovery in mid to late afternoon. Sunlit leaves of the understorey *Acacia* achieved higher values of g_s in late afternoon than at any other time during the day. Conversely, the sunlit leaves of the co-dominant *Acacia* rose to a midday maximum in g_s prior to a steady decline through the afternoon.

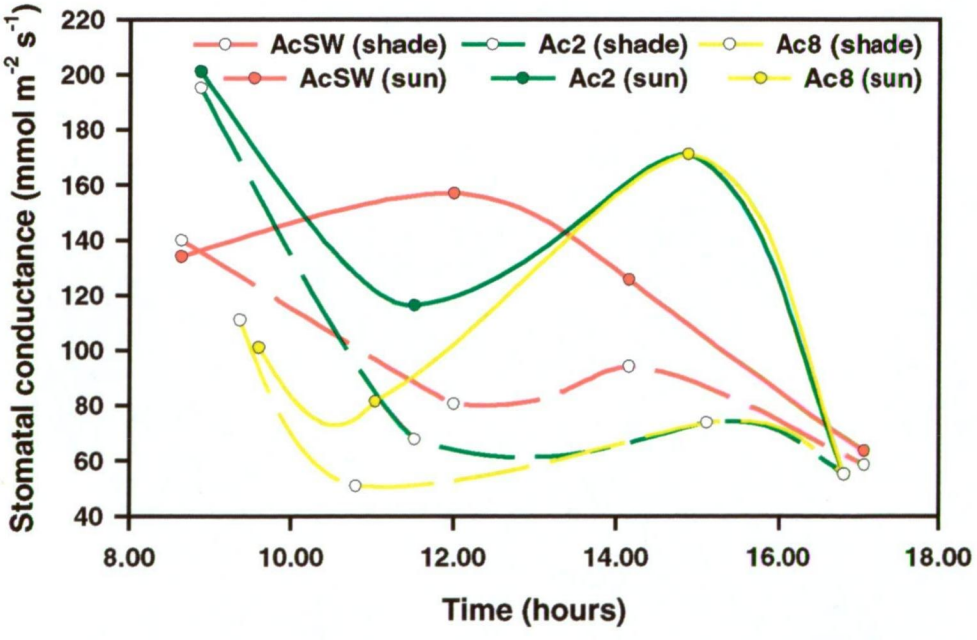


Figure 7.10 The diurnal course of stomatal conductance measured with the LI 1600 porometer on 22/2/96 for sunlit and shade leaves of co-dominant (AcSW), subdominant (Ac2) and understorey (Ac8) *A. dealbata*. Foliage was measured on four occasions throughout the day.

Sunlit upper canopy leaves of *A. dealbata* were observed to close around the rachis in the mid-morning under high PPFD. Leaf closure was associated with the timing of reduction in leaf water potential. Such leaves generally exhibited very low stomatal conductance (data not shown).

When the entire pre-midday data set was analysed (in order to exclude hysteresis associated with afternoon measurements - *sensu* White 1996), there was a significant effect of species ($p < 0.01$) and time ($p < 0.001$), but no interaction. For the same data set, SAS GLM analysis did not return significant relationships between g_s and the three potentially driving physical variables, PPFD, T_a and h ($p > 0.05$) for either species. This result was most likely due to the limited nature of the data set (ie the capacity to vary a single weather variable and hold the remainder constant) rather than a reflection of the nature of the interaction between g_s and these variables.

7.3.4 Photosynthesis

During light response curve measurements, upper canopy foliage of co-dominant trees of both species returned maximum values of A of approximately 20 μmol CO_2 m^{-2} s^{-1} as did lower canopy foliage of a sub-dominant eucalypt (Figure 7.11). Lower canopy foliage of a co-dominant *Acacia* achieved maximum A of 11 μmol CO_2 m^{-2} s^{-1}. When foliage from upper and lower crowns of co-dominant *E. nitens* and *A. dealbata* were compared (Table 7.3), maximum A decreased with canopy depth. Leaf temperature normally rose during measurement (as PPFD was reduced from 1500 – 50 μmol m^{-2} s^{-1}) and was strongly correlated with marked reductions in stomatal conductance (eg for a co-dominant *E. nitens*, T_l rose from 20.8 – 24.5°C and g_s fell from 520 mmol m^{-2} s^{-1} – 130 mmol m^{-2} s^{-1}; $r^2 = 0.85$, $p < 0.001$, regression analysis).

Data for the two diurnal measurement days and for upper crown foliage measured on 8/03/96 are summarised in Table 7.4. *E. nitens* returned higher average *A* on all measurement days though maximum recorded values for individual leaves of both species were similar (25.4 μmol CO_2 m^{-2} s^{-1} and 25.2 μmol CO_2 m^{-2} s^{-1} for *E. nitens* and *A. dealbata* respectively). Stomatal conductance (measured with the LCA-2) was similarly higher for *E. nitens* than *A. dealbata.*

On 8/3/96, *E. nitens* had higher *A* in the morning than in the afternoon for each crown stratum. *A* decreased with depth at both measurement times (Table 7.4). The lowest average values of *A* for *A. dealbata* were recorded in the bottom third of the crown and did not differ between morning and afternoon. In the upper crown, *A* for the morning sample was significantly less than in the afternoon ($p< 0.01$; *t*-test) and was exceeded by values in the mid-crown at that time. *A* was greater for *E. nitens* than *A. dealbata* for all crown zones and measurement times except for the afternoon measurements in the upper crown zone. During that measurement series, PPFD was reduced in *E. nitens* (but not for *A. dealbata*) by cloud cover.

7.4 Discussion

During the measurement period, soil moisture remained high and above the level expected to elicit a strong stomatal closing response in *E. nitens* (White, 1996). Atmospheric demand was low (calculated from Licor 1600 measurements of T_a and h) and generally at levels associated with high stomatal conductance in eucalypts (Dye and Olbrich 1993; White 1996). Whilst measurement of leaf responses over a full range of soil and atmospheric stresses was consequently not possible, patterns of plant response to physical conditions typical of the site could be identified.

The two species responded similarly to soil and atmospheric demand, though responses of *A. dealbata* were more marked. *A. dealbata* exhibited more negative pre-dawn water

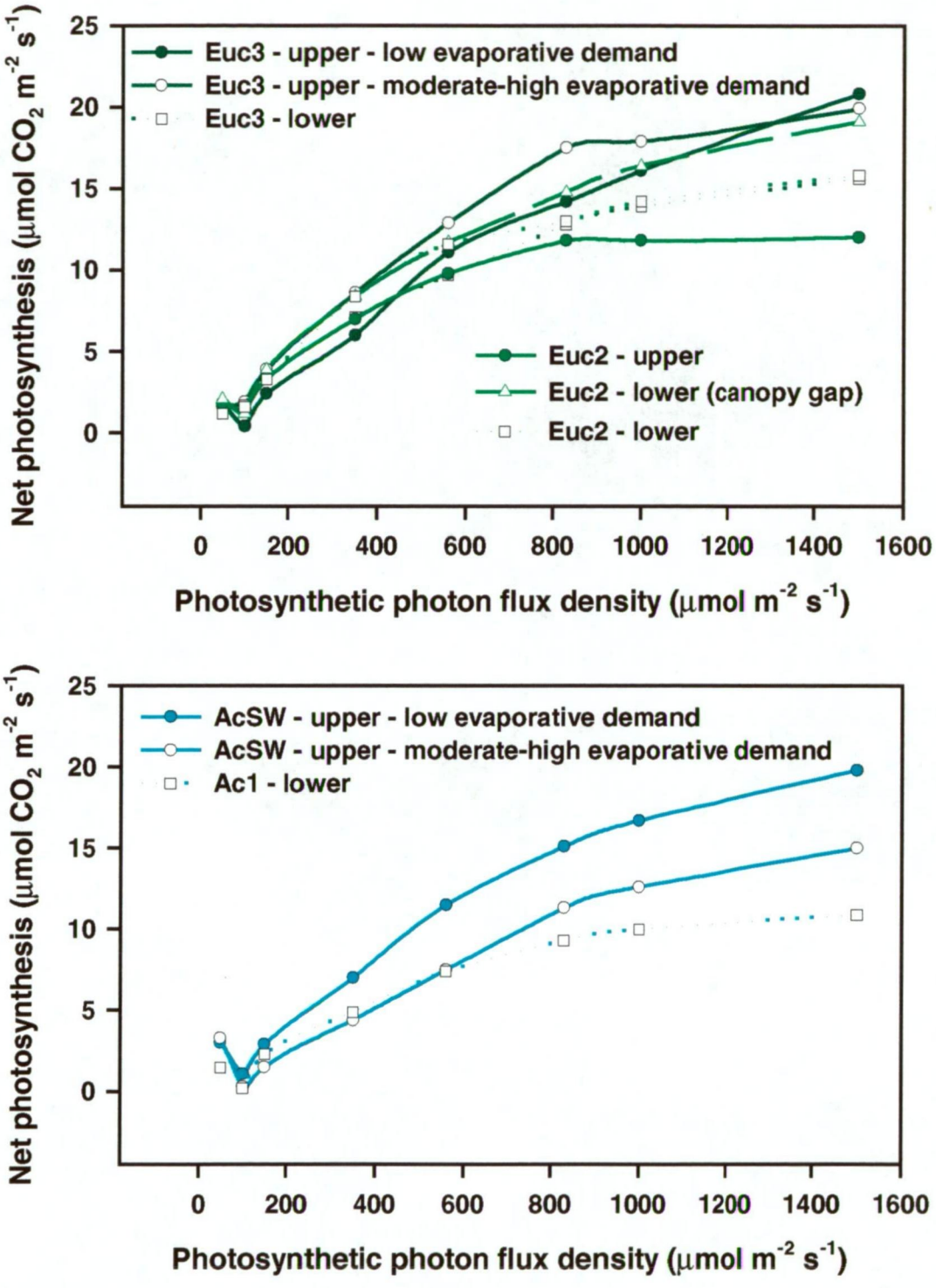


Figure 7.11 The relationship between photosynthetic photon flux density (PPFD) and net photosynthesis (*A*) measured with the ADC LCA2 on single leaves under controlled conditions of PPFD imposed at the leaf surface with an external light source and neutral density filters for (a) *E. nitens* and (b) *A. dealbata*. Leaves from both the upper and lower canopy, representing non-limiting and limiting light environments, were measured.

Table 7.2 Summary of PPFD and g_s data described by Figures 7.8 and 7.9.
Values are averages of point measurements.

	13-Feb-96			13-Mar-96		
ID	Time (hours)	Q μmol m^{-2} s^{-1}	g_s mmol	Time (hours)	Q μmol m^{-2} s^{-1}	g_s mmol
Euc2	8:38	1908	228	8:52	1735	321
	10:15	1563	238	13:10	2017	146
	12:20	1850	173	15:55	380	105
	14:40	1445	207			
	16:48	920	153			
	17:45	1267	144			
	18:40	27	40			
EucNW	8:47	1269	175			
	10:22	1669	162			
	12:35	2057	234			
	14:46	667	102			
	17:00	431	66			
	17:51	78	52			
	18:30	38	30			
Euc1	8:55	1968	238			
	10:29	1348	195			
	12:43	1563	281			
	14:55	1960	177			
	17:06	621	72			
	17:56	79	57			
	18:33	23	38			
AcSW	9:18	1382	77	9:15	1690	123
	10:43	1530	182	13:22	1423	158
	13:12	1587	119	13:58	372	95
	15:10	963	128			
	17:26	104	44			
	18:08	15	27			
Ac2	9:06	1376	137			
	10:35	1952	195			
	13:00	1157	133			
	15:02	865	171			
	17:17	62	50			
	18:05	49	23			

Table 7.3 Summary of variation among crown zones of physical and physiological variables measured with the LCA-2 on codominant trees. Values are averages of point measurements.

Species	Crown zone	Measurement time	Cuvette humidity %	PPFD $\mu mol\ m^{-2}\ s^{-1}$	T_a °C	T_l °C	g_s $mol\ m^{-2}\ s^{-1}$	A $\mu mol\ m^{-2}\ s^{-1}$
E. nitens	upper	mid-morning	44.90	995	24.35	23.40	0.46	16.58
		post-noon	20.32	438	27.94	27.26	0.11	6.44
	middle	mid-morning	38.55	670	26.10	24.75	0.35	12.67
		post-noon	25.01	614	29.24	28.31	0.16	10.80
	lower	mid-morning	31.92	874	27.43	26.73	0.24	9.68
		post-noon	20.04	748	26.44	26.40	0.12	6.61
A. dealbata	upper	mid-morning	28.99	974	27.61	27.31	0.20	3.47
		post-noon	30.32	1082	30.46	29.86	0.21	10.64
	middle	mid-morning	25.10	805	28.07	27.69	0.16	4.16
		post-noon	13.47	783	27.80	28.20	0.07	1.86
	lower	mid-morning	24.98	183	29.43	27.78	0.17	1.58
		post-noon	9.28	21	26.27	25.67	0.04	1.58

Table 7.4 Summary of physical and physiological variables measured with the LCA-2 on single leaves for three days in the 1995-96 and 1996-97 growing seasons. All data are taken from sunlit leaves in upper tree crowns and are daily averages of point measurements.

Date/Time	Species	Cuvette humidity %	PPFD $\mu mol\ m^{-2}\ s^{-1}$	T_a °C	T_l °C	g_s $mol\ m^{-2}\ s^{-1}$	A $\mu mol\ m^{-2}\ s^{-1}$
08-Mar-96	*A. dealbata*	31	704	24.6	24.0	0.26	8.04
6:00-16:45	*E.nitens*	35	751	25.0	24.1	0.29	15.37
13-Mar-96	*A. dealbata*	30	1019	28.8	28.4	0.20	6.46
8:50-16:00	*E.nitens*	34	742	26.0	25.2	0.30	11.97
17-Jan-97	*A. dealbata*	36	1345	26.0	26.1	0.27	8.07
07:00-13:20	*E.nitens*	43	1419	26.2	25.9	0.38	19.10

potentials as soils dried and reduced stomatal conductance earlier in the day than *E. nitens* (responding to more rapid diurnal reduction in leaf water potential). Leaf water potential minima were comparable for the two species but maximum stomatal conductances were lower for *A. dealbata*. Maximum values of net photosynthesis were also similar for the two species, but *A. dealbata* had values close to maximum for a much briefer part of the day than *E. nitens*.

The pre-dawn water potential data indicated that as the soil dried, *A. dealbata* was less able than *E. nitens* to completely rehydrate overnight and thus is likely to have occupied a shallower part of the soil profile (Reich and Hinckley 1989). Pioneer Australian *Acacia* spp in general have a shallow rooting habit (e.g. *A. mearnsii*; Khanna 1997). Over a diurnal cycle, leaf water potentials of *A. dealbata* fell to minima earlier than *E. nitens*. This was the case even when trees fully rehydrated overnight (indicated by similar ψ_{max} between species). Consequently, there was an indication of reduced efficiency (compared to *E. nitens*) in transporting water from the soil - root interface to the leaves of *A. dealbata*. This was also reflected in the sapwood area:leaf area relationships established in Chapter 3 (*sensu* Zimmermann and Milburn 1982) and the sapwood volume fraction data presented in Chapter 6.

Data collected from diurnal measurements indicated that the maximum photosynthetic rate of both species was approximately 25 μmol CO_2 m^{-2} s^{-1}, indicative of early successional species adapted to high light environments and requiring rapid early growth to colonise space (*cf* Chesson and Warner, 1981). Similar maximum photosynthetic rates have been reported elsewhere for *E. nitens* (Battaglia et al. 1996; 22 μmol CO_2 m^{-2} s^{-1}, Pinkard and Beadle 1998; 23 μmol CO_2 m^{-2} s^{-1}), but there is a dearth of photosynthetic data published for comparable *Acacia* spp. Brodribb and Hill (1993) measured a maximum of 12 μmol CO_2 m^{-2} s^{-1} for phyllodes (< 10 μmol CO_2 m^{-2} s^{-1} for leaves) of *Acacia melanoxylon*, a

species which establishes in disturbed environments (particularly canopy gaps) and may be present as a dominant climax species in wet temperate forests in south-east Australia. This value for *A. melanoxylon* is comparable to the mid-crown foliage maximum *A* of 11 μmol CO_2 m^{-2} s^{-1} for codominant *A. dealbata* in the present study.

Relationships developed in light response curves between PPFD and *A* for upper canopy foliage of both species were curvilinear. There was no evident plateau of *A* beyond a saturating light intensity as is apparent in the rectangular hyperbola (eg Doley 1978) or Blackman response (eg. Thornley and Johnson 1990) that are normally used to describe light response curves of a single leaf. Leaf temperature rose markedly over the period of measurement of most light response curves and this may have caused a reduction in *A*. The associated stomatal closure may have been caused by increasing vpd (due to rising temperature) in the leaf cuvette (Idso et al. 1988) rather than a response to reducing PPFD, but the effects of the two variables could not be separated. Furthermore, a rise in temperature is likely to have increased respiration which may also have influenced values of *A* measured at light intensities under 1500 μmol m^{-2} s^{-1} (the PPFD at the first measurement, after which leaf temperature was observed to rise).

Light saturated values of *A*, determined from light response curves, were lower for lower canopy foliage than for upper canopy foliage in both *A. dealbata* and *E. nitens*, though the reduction was more pronounced in *A. dealbata*. It is possible that this interspecific difference reflected the more limiting light environment at the base of the *Acacia* crown (see Chapter 4) rather than an inherently greater potential for photosynthetic acclimation in that species and, hence, shade tolerance (*sensu* Givinish, 1987). However, the absence of *E. nitens* foliage in this canopy stratum may also have reflected that species' inability to persist under very low light conditions.

A. dealbata established after *E. nitens* was planted at the site (P. Naughton, pers. comm.) and this was indicated by the species diameter distribution data in Chapter 2 (*sensu*

Yokozawa, 1996). That acacias emerge from the soil after the *E. nitens* seedlings are planted suggests that the former will be at an initial competitive disadvantage: trees of the same species (or occupying a similar niche) that occupy a lower crown class are at higher risk of mortality (Ward and Stephens, 1996). However, at the experimental site, co-dominant acacias and eucalypts were recorded growing side by side, surrounded by suppressed trees of both species at canopy closure. The rapid early above-ground growth of *A. dealbata* that permits the attainment of a co-dominant position at canopy closure may be at the expense of below-ground investment. Data from previous chapters indicate that *A. dealbata* is more competitive in younger stands than the one considered in the experiments described in this chapter. It is likely that the competitive consequences of conducting inefficiencies and rooting depth are less marked in younger stands due to the lower water use of such stands, shorter distances for water to travel from the soil to the leaves, and the relatively shorter time available for *E. nitens* to explore deeper parts of the soil profile. The resource allocation strategy that facilitates *A. dealbata* reaching an early co-dominant canopy position may subsequently be limiting through the imposition of seasonal water stress. The absence of a significant difference in ψ_{max} for *A. dealbata* and *E. nitens* in the younger stand at Site 4 supports this hypothesis.

With respect to the hypotheses stated at the beginning of this chapter, *A. dealbata* does not have lower maximum photosynthetic rate than *E. nitens* but is more water limited on a diurnal basis. Both *E. nitens* and *A. dealbata* exhibit autecological responses typical of early successional light adapted species.

Chapter 8. A review of competitive interactions between *E. nitens* and *A. dealbata* and their management and ecological implications

8.1 Introduction

This thesis has considered competition between plantation *E. nitens* and naturally regenerating *A. dealbata*. The study was conducted in a commercial plantation typical of those being established for short-fibre production in northern and south-eastern Tasmania. This plantation system also represents a simple analogue of more complex natural wet eucalypt forests in south-eastern Australia where *A. dealbata* is a significant component of the young forest canopy. The first aim of the study was to identify the presence or absence of competition. Having done this, the timing, mechanisms and extent of competition were investigated with a view to defining appropriate operational prescriptions for the management of that competition. Additionally, the *Acacia/Eucalyptus* interaction provided an unusual opportunity to study a potentially competing two-species tree system. Whilst competition *per se* may be one or two sided in such a system, this thesis was written from the perspective of plantation production and thus the effect of *A. dealbata* on *E. nitens* growth and productivity was of primary interest.

The distribution of naturally regenerated *A. dealbata* in young plantations is related to distribution of mature trees in the original forest and the associated distribution of their seed. *A. dealbata* is known to set seed at age three to five years. Therefore, seed load and seed distribution are likely to be increased at the beginning of a second eucalypt rotation compared to at initial site establishment if sufficient numbers of trees survive long enough in the canopy to set seed. From this perspective of repeated site infestation by *A. dealbata*,

this chapter summarises the competitive interactions between the two species and discusses both the implications for plantation management and for the life history of *A. dealbata* within the context of current ecological theory.

8.2 Summary of results

8.2.1 *Acacia* distribution and interactions at the population level (Chapter 2)

The high early growth rate of *A. dealbata* combined with a high stem density in some plots resulted in their canopy closure as early as age 2 years. The various combinations of stem density and vigour of *A. dealbata* caused competition to peak at age 2 - 6 years, after which age the *A. dealbata* canopy had been at least partially suppressed. Silviculture used for site preparation and establishment were identified as important contributors to the distribution and abundance of *A. dealbata* throughout the plantation as was the pre-plantation distribution of mature seed-bearing *Acacias*. Whilst soil nitrogen status was observed to benefit from the presence of *A. dealbata*, *E. nitens* basal area was adversely affected. Reductions in plot standing volume of *E. nitens* of almost 25% (compared to plots without *Acacia* competition) were recorded at age 7 years. Competition between the species was thus indicated but soil nutrients determined not to be the primary limiting resource.

8.2.2 Stand structure and canopy architecture (chapters 3, 4 and 5)

A range of stem variables was found to be closely related to tree leaf area in both *A. dealbata* and *E. nitens*. There were only small improvements in predictive capacity gained by using basal measurements of sapwood area over cross-sectional area as the stem scaler but measurement of these variables at the base of the crown yielded generally closer relationships.

Basal area measurements were used to estimate stand leaf area in plots both with and without *A. dealbata* competition. LAI of *E. nitens* was markedly reduced in *Acacia*-infested stands compared to *Acacia*-free stands in both 8-year-old and 4-year-old plots. Most foliage of *E. nitens* was concentrated above the *A. dealbata* canopy in an 8-year old plot and vertical profiles of irradiance indicated that light transmittance was reduced most markedly at the associated transition zone between foliar concentrations of the two species.

Standard planimetry was found to have inadequate resolution for the measurement of the area of *A. dealbata* foliage. This was due to the highly dissected nature of the *A. dealbata* leaf and the consequent small size of individual foliar elements. However, larger measurement errors, associated with the habit of *Acacia* pinnae closing about the rachis, were identified and these were not able to be overcome through increases in measurement resolution. High resolution measurement of individual primary pinnae, rather than whole leaves, returned average area values of approximately twice those obtained using the standard technique. The relative contribution of *A. dealbata* to the mixed canopies was thus likely to have been substantially greater than estimated. As corrections were obtained for leaves on trees other than those for which basal area:leaf area relationships were derived, the original relationships were retained and the consequences of errors were noted and discussed.

8.2.3 Partitioning of stand water use (chapter 6)

The relative contribution by the two species to stand water use was investigated using the heat pulse velocity technique. Marked radial and axial variations in sap velocity were observed for both species, the latter source of variation being most pronounced in *Acacia* infested stands where crowns were asymmetrical. Stem diameter was used to scale individual tree estimates of water use to the stand level. Plot transpiration was estimated to be less than 1 mm day^{-1} in an *Acacia* infested 4-year old plot and up to nearly 3 mm day^{-1}

in *Acacia*-infested 8-year old plots. The level of *A. dealbata* infestation was associated with absolute plot water use and regression models predicted that in the absence of *Acacia* competition plot water use for an 8-year-old stand would approach 5-6 mm day^{-1}.

8.2.4 Foliar gas exchange and plant water status (chapter 7)

A. dealbata was less able to maintain plant water status than *E. nitens*, both seasonally as the soil profile dried, and diurnally as transpiration increased. Associated decreases in stomatal conductance reduced the relative capacity for *A. dealbata* to photosynthesise at its maximum potential rate, which was found to be close to that of *E. nitens*. Greater access to, or efficiency in transport of, water thereby provided *E. nitens* with competitive advantages over *A. dealbata* even though both species possessed equivalent leaf photosynthetic capacity under otherwise non-limiting conditions.

8.3 Implications for stand management and E. nitens productivity

E. nitens plantations on good and average quality sites are presently grown on a rotation of less than 20 years for short fibre production (Stephens and Hansard 1994). *A. dealbata* is a species recognised as favouring wet, fertile sites and is a species used as an indicator of high site quality in Tasmania (Keenan and Candy 1983). It is therefore likely to be present in significant densities on sites cleared of native forest prior to plantation establishment. Furthermore, the seed of *A. dealbata* remains viable in the soil for many decades. Thus ex-pasture sites with similar native forest history will also be affected. Fertilisation at establishment, the benefits of residual fertility on ex-agricultural sites and the nitrogen-fixing ability of *A. dealbata* combine to minimise the possibility of nutrient limitation in these plantations. Soil nutritional analyses after canopy closure in the present study support this assertion (Chapter 2).

Whilst the sites under consideration are mesic (with annual rainfall approximating annual pan evaporation), seasonal water availability is recognised as a serious potential limitation to summer growth (Nicolls et al. 1982). On the deeper soils characteristic of the older stands considered in this study, water limitation for *E. nitens* in *Acacia*-infested stands was found to be infrequent and not marked (Chapter 7). If anything, the presence of *A. dealbata* in the stand reduced stand water use below that potentially achievable by an *E. nitens* monoculture at the site (Chapter 6). It is likely that this was due to the presence of a significant component of *A. dealbata* in the tree canopy (Chapter 4) which was unable to access soil water at depth and thus maintain (on a daily time-step) stomatal conductances, and consequently transpiration rates, of the magnitude achieved by *E. nitens* (Chapter 7). This water limitation for *A. dealbata* during the growing season, coupled with interspecific differences in resource allocation and respiratory costs, may be the mechanism by which that species is eventually competitively excluded from mixed stands.

In the younger stands considered in this study, soils were generally shallower and analyses of leaf level water status and water use were sparingly undertaken. It is not possible to evaluate the potential competition for water on such sites based on the data presented in this thesis. Nevertheless, whole tree water use and leaf level data both indicate the greater ability of *E. nitens* than *A. dealbata* to obtain water from the soil profile. Thus, the latter species' ability to significantly compete with the former must be inherently questionable, except very soon after establishment when a dense *A. dealbata* population may be exploring the same upper part of the soil profile as the young *E. nitens* trees.

Competition for light remains the most important mechanism by which *A. dealbata* is able to suppress the productivity of *E. nitens* in mixed stands. Data from this thesis indicate that an initially dense *A. dealbata* population may take more than eight years to be suppressed by *E. nitens* (Chapter 2). As dominant *A. dealbata* are still present in the canopy at age eight, competition may not be excluded completely prior to harvest and thus the annual

productivity of the eucalypts will be influenced for the entire rotation. Consequently, the reduction in *E. nitens* standing volume (in *Acacia*-infested plots compared to *Acacia*-free plots) of approximately 25% at age eight years that was observed in this study is highly unlikely to be regained in the second half of the rotation. Importantly, after a certain age, manipulation of stand density will not bring about full expression of site potential. Dense canopies are characterised by comparatively shallow depths and small live crown ratios (Chapters 3, 4). When released, and growth becomes independent of density, these canopies may exhibit slow growth despite the crown being independent of density. Such a phenomenon has been identified at age 27 years for *Pinus taeda* (Dean and Baldwin 1996) but is yet to be identified for rapidly growing *E. nitens* plantations. Thus early losses in potential plantation productivity may be magnified rather than reduced over a rotation.

It is unlikely that regeneration of *A. dealbata* will be restricted to primary rotations only. Trees were observed to set seed prior to suppression by the eucalypts and the disturbance associated with tree establishment and site preparation for subsequent rotations is analogous to that experienced in native forests of which it is a component (see subsequent section). Therefore, site preparation is likely to play a major role in the success of *A. dealbata* establishment for as long as plantations are grown at a site.

Manipulation of site burning and the accurate timing of herbicide application are indicated as potential tools for the reduction of levels of competition from *A. dealbata* at and soon after plantation establishment. Minimal disturbance and restriction of fires to low intensity reduce the germination of *A. dealbata* seed (Chapters 1, 2). The complete exclusion of fire in favour of mechanical clearing, or the adoption of slash retention practices, will further limit density of *Acacia* germinants. Vegetative regrowth of *A. dealbata* by suckers will be less affected by such site preparation. The delay of knock-down herbicide application until after *A. dealbata* seedlings and suckers emerge from the soil resulted in 30% more

standing volume of *E. nitens* in 8-year-old plots at the plantation considered in this study (eg at Site 2). Furthermore, treatment of the inter-row (as well as planting mounds) with a residual herbicide may assist in the prevention of post-establishment growth of *A. dealbata.*

Finally, there may be a need to evaluate the potential use of high initial stocking of *E. nitens* at susceptible sites. Rapid growth of *E. nitens*, combined with high stocking may result in earlier canopy closure (~2 years) before *A. dealbata* can become a significant codominant in the stand and, in the interim, reduce vacant space that *A. dealbata* can colonise. Advantages gained under such a system would need to be balanced against the potential for associated compromise of post-planting weed control of *A. dealbata.*

8.4 Implications for the placement of the competitive success of *A. dealbata* within current ecological theory

Much of current ecological theory depends on the assumption that communities exist at competitive equilibrium, but this is rarely the case (Huston, 1979). Increasingly, it is recognised that plant species diversity is more influenced by chance and history than by interspecific competition (eg Hubbell and Foster 1986; Hurtt and Pacala 1995). A competitively inferior species may coexist with a superior competitor if chance or superior ability to colonise allows it to capture vacant space and if vacant space is generated often enough. Most consideration of such non-equilibrium outcomes focuses on the timing and magnitude of population size reduction and on the nature of competitive interactions (eg Huston 1979; Chesson and Warner 1981). This thesis has taken such an approach but has also considered temporal changes in competition for light and water and, to a lesser extent, nutrients.

Also important is the ability of an inferior species to persist or endure competition not just in the vegetative form but also as seed in the soil. In such cases, provided the inferior

competitor can persist long enough in the vegetative phase to produce seed, and provided seed survives in the soil long enough to provide germinants at the next disturbance interval, then coexistence may continue. This may be the case even though the rate of competitive exclusion may be high compared with the inter-disturbance interval (*sensu* Huston, 1979).

In this study, *A. dealbata* was found to be an effective early competitor but was clearly being suppressed by 8 years of age. These results are in agreement with data derived from natural systems where *A. dealbata* is frequently present only in the early stages of eucalypt forest succession following fire or disturbance. Even in the absence of competition, the species is short-lived (< 70 years). However, seed is produced when trees are young (~3 years compared to at about 10 years for competing eucalypts (New 1984; Eldridge et al. 1993). Seed longevity is marked in *A. dealbata*, with observations of germination from seeds stored in the soil for in excess of 200 years (Gilbert 1959). It is evident, therefore, that its continued representation in eucalypt forests relies on its ability to utilise a brief temporal niche (*sensu* Chesson and Warner, 1981) in young stands during which its rapid early growth allows it to match the growth of the eucalypts. Thereafter it is over-topped by the eucalypts and is competitively excluded . It subsequently continues to exist only as propogules in the soil seedbank awaiting the next cycle of disturbance and revegetation.

Connell (1978) identifies three non-equilibrium hypotheses: intermediate-disturbance hypothesis, equal-chance hypothesis and the gradual-change hypothesis. The case of the *A. dealbata-E. nitens* system is most analogous to the intermediate-disturbance hypothesis in which disturbance maintains diversity by preventing competitive exclusion. However, this does not strictly apply as *A. dealbata* is competitively excluded from the system. It is also analogous to the recruitment limitation model of Hurtt and Pacala (1995) in which a 'fugitive species' is able to persist despite being a poor competitor if it is better able to

colonise vacant space and if vacant space is generated often enough. Again, the *A. dealbata* situation stretches this hypothesis because colonisation is not carried out in any spatial dispersal sense, but by persistence in time.

Thus in the future development of ecological theory, and as the non-equilibrium models typical of disturbance-based eucalypt ecosystems gain further recognition, an additional model to those already postulated may be useful. In such a model, the occupation and reproduction of a species occupying a brief temporal niche and surviving only as propagules between disturbance cycles would be recognised as an effective competitive strategy. To some extent, such a model is already recognised in the description of annual species in desert communities which respond to precipitation rather than disturbance (Symonides 1988). *A. dealbata* is an example of a forest tree species that fills an analogous temporal niche. I propose that the competitive strategy of *A. dealbata* described above may be usefully referred to as a 'disturbance-dependent pioneer reproduction' model.

8.5 Conclusion

The above discussion has addressed the four questions asked at the beginning of this thesis in Chapter 1. The results and their interpretation allow rejection of the hypothesis on which this study was based (Section 1.3). *A. dealbata* does possess the physiological and morphological capacity to effectively compete with *E. nitens* in the plantation system. Furthermore, such competition is sufficient to significantly and markedly reduce the productivity of *E. nitens* in that system.

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